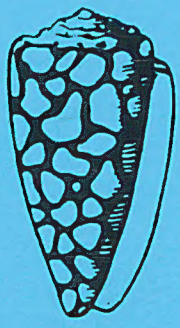
Volume 17
30 June 1996

Molluscan Research

(Formerly Journal of
The Malacological Society of Australia)



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The Malacological Society of Australasia
A.C.N. 067 894 848

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MOLLUSCS 97

Symposium on the Molluscs of the Indo-West Pacific
and Australasian Region

Rottnest Island, Western Australia
1–4 February 1997

Organised by:

The Malacological Society of Australasia Ltd.
ACN 067 894 848

The huge Indo-West Pacific and Australasian Region has a tremendous diversity of molluscs in all environments: marine, freshwater and terrestrial. This will be the first meeting to bring together malacologists and other interested scientists working on the molluscs of the region.

The symposium will be held at the Rottnest Environmental Education Centre at Rottnest Island, off the coast of Perth, Western Australia from 1 to 4 February 1997.

The first two days of the conference, Saturday 1 and Sunday 2 February, will be devoted to scientific sessions, as will Tuesday, the 4th. Excursions will be held on Monday, 3 February.

Rottnest Island is on the central west coast of Western Australia, where there is a mixture of temperate, tropical and Western Australian endemic molluscs. An island tour with the opportunity to explore the local rocky shore habitats will be organised for Monday, 3 February.

The symposium will be held over a weekend so that Australian participants can obtain the cheapest airfares (which require a stay including a Saturday night).

The Malacological Society of Australasia expects to make limited travel support available to some student members living in Australasia who present a paper or poster.

Three symposia are planned:

- Molluscs of environmental or economic importance
- Evolutionary studies of molluscs
- Contributed paper sessions

Posters are also welcomed as an alternative to papers. The symposium is open to papers and posters on all aspects of Indo-West Pacific and Australasian molluscs, whether marine, freshwater or terrestrial.

Participants are encouraged, but not required, to publish the papers presented in *Molluscan Research*, the journal of The Malacological Society of Australasia. Papers submitted to *Molluscan Research* will be subject to the normal editorial review process.

Post conference tours

- Many of the delegates will be visiting Western Australia for the first time. There will be a four day postconference tour to the Cape Nautraliste-Cape Leeuwin area on the southwestern corner of the state, pending sufficient interest. More information will be available in the second announcement.
- Information will also be sent in later announcements on commercial day trips available from Perth.

To register for the mailing list for further announcements please write to:

Dr FE Wells
Western Australian Museum
Perth WA 6000 Australia

Fax: 61 9 328 8686

Book review

Taylor, JD (Editor). 1996. Origin and Evolutionary Radiation of the Mollusca. Oxford University Press. ISBN 0 19 854980 6.

The Malacological Society of London is one of the oldest and most respected such societies in the world, best known for its publication of the *Proceedings of the Malacological Society of London,* reformatted in recent years as the *Journal of Molluscan Studies.* The Society celebrated its centenary in September 1993 with a symposium on the "Origin and evolutionary radiation of the Mollusca" held at the Natural History Museum in London. The present book is a compilation of some of the papers presented at the symposium.

The last 20 years has seen a considerable increase in research into the origin and evolutionary radiation of the Mollusca as new techniques in cladistic analysis and molecular methods became available and routinely applied. Results obtained from these studies led to a reappraisal of both old and new data obtained from anatomical studies and examinations of the fossil record. The result has been a dynamic re-evaluation of our understanding of the origin of the Mollusca and the evolutionary paths undertaken by groups within the molluscs.

The centenary symposium brought together leading malacologists from throughout the world to present the results of their work and to discuss the issues raised. The resulting volume does not give final answers, but rather appears as an up to date snapshot of our understanding at the moment. Evolutionary papers presented at the Unitas meeting in Vigo last (northern) summer showed that research in this field is actively continuing.

Papers in the book are grouped into three sections. The first section of ten papers discusses relationships between molluscs and other phyla (Turbellaria, Annelida, Sipuncula) or relationships at higher taxonomic levels. Papers on molluscan groups utilise a variety of approaches, including comparative anatomical studies of shell pores, sperm ultrastructure, phylogenetic analysis, the fossil record and biogeography.

The second, and largest, section of 27 papers examines gastropods form a variety of viewpoints. The first paper, by Ponder and Lindberg, reviews our current understanding of gastropod phylogeny and outlines an approach for future studies. Several papers examine general characters of gastropods or higher taxa within the Gastropoda such as the significance of cleavage patterns for reconstructing gastropod phylogeny, initial radiation of the Archaeogastropoda, lepetid limpets, trochoideans, stylommatophorans, and neogastropods. Other papers examine in detail groups at the family or lower level, including Cypraeidae, the *Littorina saxatilis* complex, sacoglossans, *Haminaea navicula,* Clausiliidae, Ellobiidae, *Albinaria,* and *Calliostoma zizyphinum.* One paper contrasts developmental strategies and speciation in prosobranchs. This section contains a wealth of information at all levels within the group.

The final, and shortest, section brings together three papers on bivalves and a short one on scaphopods. The first two contributions on bivalves discuss the evolution of the class, and the third examines the phylogenetic significance of anatomical features of bivalve veligers.

There are no papers on the other molluscan classes. To a large degree this absence probably reflects the relative lack of work in them.

The book is superbly produced, and a substantial credit to the symposium organiser and volume editor, John Taylor of the Natural History Museum. It is a landmark contribution to malacology and will be heavily used by researchers examining many aspects of the biology of molluscs, particularly evolutionary studies.

Fred E Wells

Moll. Res. 17: 3–20 (1996).

Comparative study on gill morphology of gastropods from Moreton Bay, Queensland

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Key words: molluscs, ctenidia, SEM/LM

Abstract

This paper reports the gill morphology of seven common gastropods from Moreton Bay, southeastern Queensland, to test the level of difference in gill structure between major taxa. The investigated species include representatives of the clades Patellogastropoda, Neritimorpha and Vetigastropda as well as representatives of the more 'advanced' Caenogastropoda. Examination by SEM and LM revealed that the external gill structure of the investigated caenogastropods (including *Planaxis sulcatus*, *Littoraria articulata*, *Bembicium auratum* and *Morula marginalba*) shows basic uniformity. The gill filaments are composed of a clearly defined ridge and an extended sheet of non-ciliated cells. The gill filaments of these species differ in the shape of the filaments (corrugated, triangular or rounded) and the presence of secretory cells. The gills of the limpet *Patelloida mimula* and neritid *Nerita chameleon*, representatives of the clades Patellogastropoda and Neritimorpha respectively, are both triangularly shaped, but differ by the presence of paddle shaped cilia in the former species and secretory cells in the latter. The gill morphology of the vetigastropod trochid *Austrocochlea constricta*, characterized by blade shaped filaments covered with nodules and a striped pattern of ciliated cells, showed the least similarities with the other investigated species.

Introduction

Gills are the principal organs of respiratory gas exchange in molluscs, and additionally perform a trophic function in most bivalves and some gastropods. Where primary gills (ctenidia) have been lost, secondary gills have evolved in some molluscan groups from modifications of the mantle surface (Yonge, 1952). Although the histological structure of gastropod gills has been well described (Hyman, 1967; Voltzow, 1994), the number of studies on gastropod gill morphology is very limited. A few papers have been published on the ultrastructure of ctenidia of bivalves (Nakao, 1975; Porvaznik *et al.*, 1979; Fisher and Hand, 1984; Giere, 1985 and Le Pennec *et al.*, 1988), while Schipp *et al.* (1979) have dealt with the ctenidia of the cephalopod *Sepia officialis*. Russell-Hunter (1988) described the functional morphology of the ctenidia of chitons, but did not detail the ultrastructure of the gill filaments. Recently, however, Fischer *et al.* (1990) have presented a detailed SEM/TEM account of the gills of *Chiton olivaceus*. The few species studied in these papers have little in common as they belong to widely separated molluscan classes. The only ultrastructural studies on gastropod gills dealt with the secondary gills of the opisthobranchs *Phyllidia pulitzeri*, *Archidoris pseudoargus* and *Peltodoris atromaculata* (Wägele, 1984; Jonas, 1986), the pulmonate *Siphonaria capensis* (De Villiers and Hodgson, 1987) and the patellogastropod *Patella vulgata* (Nuwayhid *et al.*, 1978). These species belong to different gastropod clades and, surprisingly, literature on 'prosobranch' gill morphology is lacking.

Table 1. Interspecific relationships between the investigated species taken into account the revised classification as reviewed by Haszprunar (1988) and Bieler (1992).

CLASS	SUBCLASS	ORDER	SUPERFAMILY	FAMILY	SUBFAMILY	GENUS	SPECIES
Gastropoda	Prosobranchia	Patellogastropoda	Patelloidea	Acmaeidae		*Patelloida*	*P. mimula*
		Neritimorpha	Neritoidea	Neritidae		*Nerita*	*N. chameleon*
		Vetigastropoda	Trochoidea	Trochidae		*Austrocochlea*	*A. constricta*
		Caenogastropoda	Littorinoidea	Littorinidae	Littorininae	*Littorina*	*L. articulata*
					Lacuninae	*Bembicium*	*B. auratum*
			Cerithioidea	Planaxidae		*Planaxis*	*P. sulcatus*
			Muricoidea	Muricidae		*Morula*	*M. marginalba*

In the present study the ctenidia of a number of common gastropods from Moreton Bay were investigated with SEM and LM. The purpose of selecting a range of gastropods was to test, for the first time, the level of difference in gill ultrastructure between major taxa [*e.g.* clades such as Patellogastropoda (*Patelloida mimula*), Neritimorpha (*Nerita chameleon*) and Vetigastropoda (*Austrocochlea constricta*) versus the more 'advanced' Caenogastropoda, including representatives of the families Muricidae (*Morula marginalba*), Planaxidae (*Planaxis sulcatus*) and Littorinidae. By examining two local species of the caenogastropod family Littorinidae (a world-wide and well defined group), results could be compared at the intergeneric level (*Littoraria articulata* versus *Bembicium auratum*) and also viewed in relation to the various niches occupied by littorinids within the study area. The results will be discussed in the context of the systematics of the species involved (Table 1), taking into account the latest reorganisation of the 'prosobranch' classification as reviewed by Haszprunar (1988) and Bieler (1992).

Materials and methods

Animals: All investigated species were collected during low tide at Wellington Point on the western shore of Moreton Bay, South-East Queensland, where they inhabit the intertidal zone on rocky shores and jetty piles (Eertman and Hailstone, 1988). The animals were transferred to the laboratory, where they were held in 10 l aquariums filled with seawater taken from the collection site. The water was continuously aerated and maintained at a constant temperature of 22 °C. The animals were allowed to acclimatize to laboratory conditions for at least 48 hours before the gills were removed.

Scanning Electron Microscopy: The shell of a species was carefully cracked with a vice, and then the animal removed. The gills were excised and rinsed in freshly filtered seawater, before being left in 16 % glycerol for 1 hour to remove the bulk of mucous deposits (Mariscal *et al.*, 1978). The gills were then sonicated (Unosonics sonicator) for one or two periods of 30 seconds in freshly prepared 16 % glycerol to remove any remaining mucous. After a further rinse in fresh seawater, the gills were fixed for 2 hours in 3 % glutaraldehyde, prepared with 0.1 M phosphate buffer (osmotically adjusted with 5 % sucrose, to prevent tissue damage caused by osmotic shock). As mucous particles sometimes remained attached to the surface of the gill filaments, the gills were sonicated for an additional period of 30 seconds in 5 % (v/v) NH_4OH after fixation. After a final rinse in 0.1 M phosphate buffer, the tissue was dehydrated in a graded series of ethanols and critical point dried after two changes of amyl acetate. The gills were gold-coated in a SPI sputter coater and examined using a Philips SEM 505.

Transmission Electron Microscopy: The gills were fixed for 2 hours in 3 % glutaraldehyde, prepared with 0.1 M phosphate buffer (with 5 % sucrose added). After a rinse in phosphate buffer, they were postfixed for 80 minutes in phosphate buffered 1 % osmium tetroxide. Subsequently the gills were

rinsed again in phosphate buffer, dehydrated in a graded series of ethanols, and embedded in Spurr's epoxy medium (Spurr, 1969). Ultrathin sections were cut on a LKB UM III, and stained with lead citrate and uranyl acetate (30 s Pb – 60 s UA – 30 s Pb) (Daddow, 1983). The sections were examined with a Hitachi H300 transmission electron microscope at 75 kV.

Light Microscopy: The excised gills were rinsed in freshly filtered seawater, before being fixed overnight in 10 % neutral buffered formalin. The next day the gills were washed in distilled water, then dehydrated in a graded series of ethanols (70 %, 90 % and 100 %, for periods of 30 minutes each). This was followed by two thirty minute periods of immersion in toluene, after which the gills were embedded in wax. Subsequently, 6 µm thick sections were cut on a Spencer Rotary 828 microtome. After completion of the cytochemical tests the sections were examined and photographed under an Olympus light microscope fitted with a photo-automat.

Cytochemistry: Schiff's periodic acid test was performed on 6 µm thick light microscopic sections to determine the presence of mucopolysaccharides in secretory cells (Lillie, 1964). Ayoub-Shklar's (1968) method for keratin and prekeratin was performed on 6 µm thick light microscopic sections to establish the type of connective tissue present in the gill filaments. Mayer's haematoxylin – eosin alcoholic stain was used when preparing routine overview sections.

Figure 1. LM micrograph of the gill of *Austrocochlea constricta*. The nature of the connective tissue was determined with Ayoub-Shklar's (1968) method for keratin and prekeratin. The largest proportion of the connective tissue consists of collagen (c), which stains darkest. The somewhat lighter stained areas surrounding the collagen consist of prekeratin (p).

Results

Austrocochlea constricta (Vetigastropoda, Trochidae)

External gill structure: The trochid *A. constricta* has a single bipectinate gill, positioned on the left side of the mantle cavity. The anterior third of the gill is supported by a collagenous rod, which attaches the gill to the mantle wall. The filaments of the outer row are shorter (1.1 ± 0.1 mm) than those of the inner row (3.2 ± 0.1 mm). Towards the anterior and posterior ends of the gill, the filaments gradually decrease in length (Plate 1A). Each gill filament is blade-shaped, and its dorsal margin covered with long cilia (Plate 1B + 1C). A row of nodules occurs on both sides of individual gill filaments, each nodule being covered with long cilia, with the exception of the basal margin (Plate 1B, 1C + 1E). Alternating rows of ciliated and non-ciliated cells give each filament a striped appearance. The rows of ciliated cells, which are usually 3 to 4 cell-layers wide, extend from the base of a nodule across the filament towards the outer margin (Plate 1C). These cilia, which are shorter than those covering the nodules, appear in small tufts (Plate 1D).

Internal gill structure: Transverse sections through gill filaments reveal a single layered epithelium, with columnar epithelial cells that are 13.8 ± 0.7 µm long (20 cells measured). Each filament is supported axially by a double layer of collagenous connective tissue, enclosing the haemocoelic space (Plate 2A). This double layer of connective tissue thickens towards the anterior end of the filament where both layers join, forming the main haemolymph canal. The connective tissue layer surrounding the main haemolymph canal consists of an inner layer of collagen and an outer layer of proteinaceous prekeratin (Figure 1). Ciliated cells are noticeably more electron-dense than non-ciliated cells (Plate 2B). Each cilium is composed of a standard 9+2 axoneme, a basal body and associated ciliary rootlets (Plate 2B). All ciliated and non-ciliated cells exhibit microvilli on their apical surface. Although individual microvilli were not discernible under SEM, their presence is clearly demonstrated in TEM sections (Plates 1F and 2B). Microvilli measure 1.1 ± 0.1 µm in length (20 cells measured), and are surrounded by an electron-dense glycocalyx (Plate 1F). All epithelial cells, whether ciliated or non-ciliated, have a round to oval nucleus in the centre or basal half of the cell. Mitochondria seem to be concentrated in the apical half of each cell. Gap junctions between cells, containing septate desmosomes, are associated with membranes of adjoining epithelial cells and presumably serve as attachment zones (Plate 1F).

Gill filament nodules are triangularly shaped in longitudinal sections and broadly attached to the filament (Plate 2C). Each nodule has a maximum width of about 40 µm and is approximately 33 µm high. Each nodule has a coating of columnar epithelial cells of which the apical ones are ciliated. The function of these nodules remains unclear. Although some sensory function could perhaps be expected, no obvious sensory cells were observed inside the nodule.

Two types of secretory cells could be distinguished in the gills of *A. constricta*: mucous secreting cells and secretory cells containing large electron-dense vesicles. The mucous secreting cells have a typical goblet cell appearance and are located amidst the epithelial cells (Plate 2D). The cells are oval with a narrow apical neck facing towards the surface of the gill filament. The cells, which react PAS-positively, are filled with mucus in one large vacuole. The mucus appears as finely granulated secretions of low electron density. The nucleus and cell organelles are confined to a narrow area near the lateral and basal areas of the plasma membrane. The second type of secretory cell is not restricted to a specific location in the gill. It can be found: (1) bordering the surface of the filament, (2) totally enclosed by epithelial cells (Plate 2E), or (3) inside the nodules that cover the gill filaments. This type of secretory cell shows many characteristics associated with cells that have high metabolic activity. Mitochondria with well developed cristae are present throughout the cell. A rough endoplasmic reticulum (RER) occupies most of the cytoplasm (Plate 2F), indicating a high level of protein synthesis. Secretory vesicles, budded from the Golgi cisternae, presumably fuse to form the larger vesicles. All secretory vesicles, irrespective of size, are clearly surrounded by a membrane. The function and structure of these secretions remain unknown, although the cells react negatively to PAS tests, indicating that mucopolysaccharides are not present. In cells that border the gill surface, release of secretory products by exocytosis could be observed.

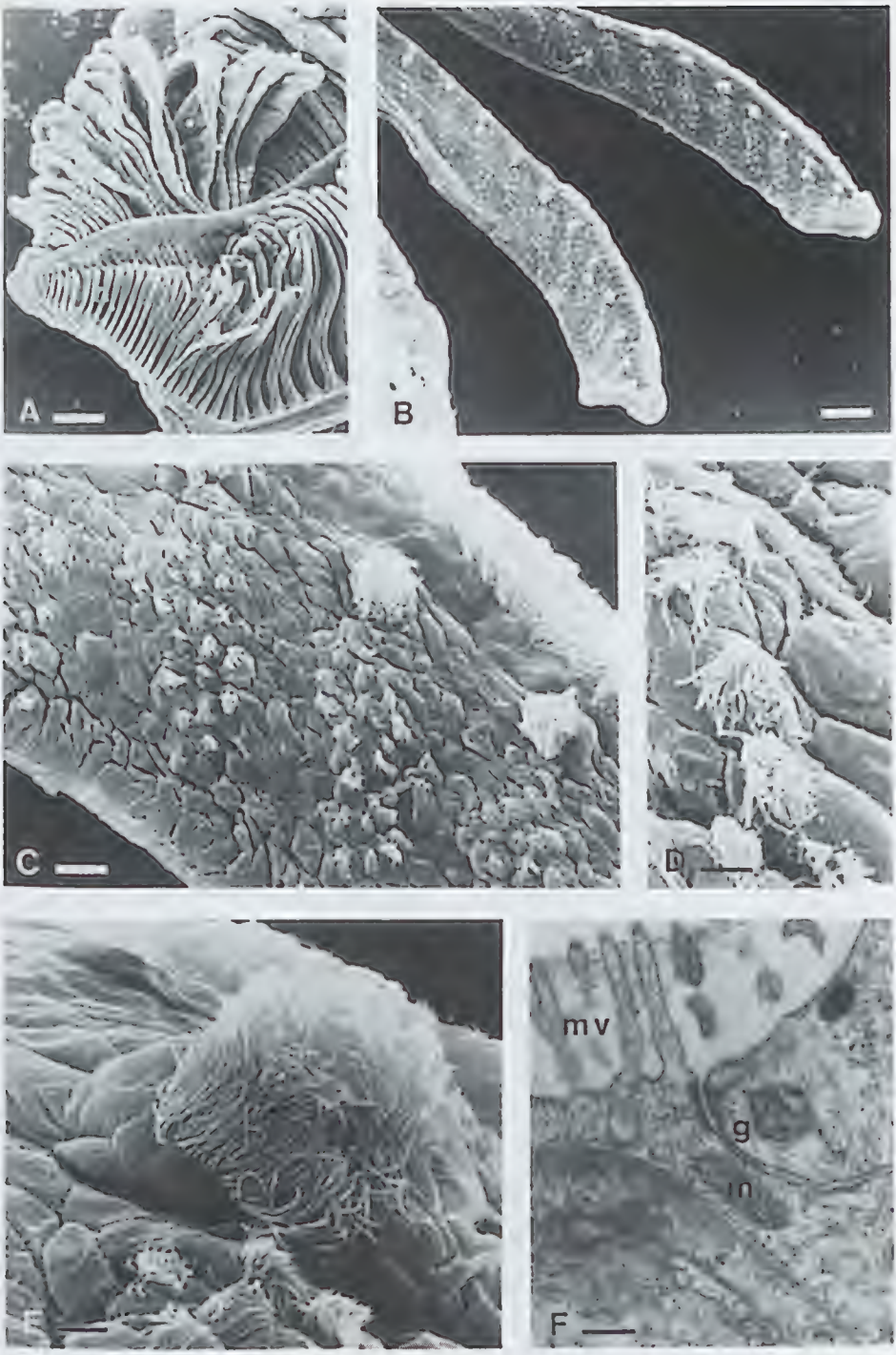

Plate 1. SEM and TEM micrographs of the gill *of Austrocochlea constricta.* A. General view showing anterior region of bipectinate gill. Bar = 0.16 mm. B. Individual gill filaments, showing rows of nodules and striped pattern of ciliated cells. Bar = 0.12 mm. C. Detail of gill filament. Bar = 15 µm. D. Detail of area with ciliated and non-ciliated cells. Bar = 4 µm. E. Nodule. Bar = 3.5 µm. F. Detail of non-ciliated cell with microvilli (mv), mitochondria (m) and gap-junction (g). Bar = 0.2 µm.

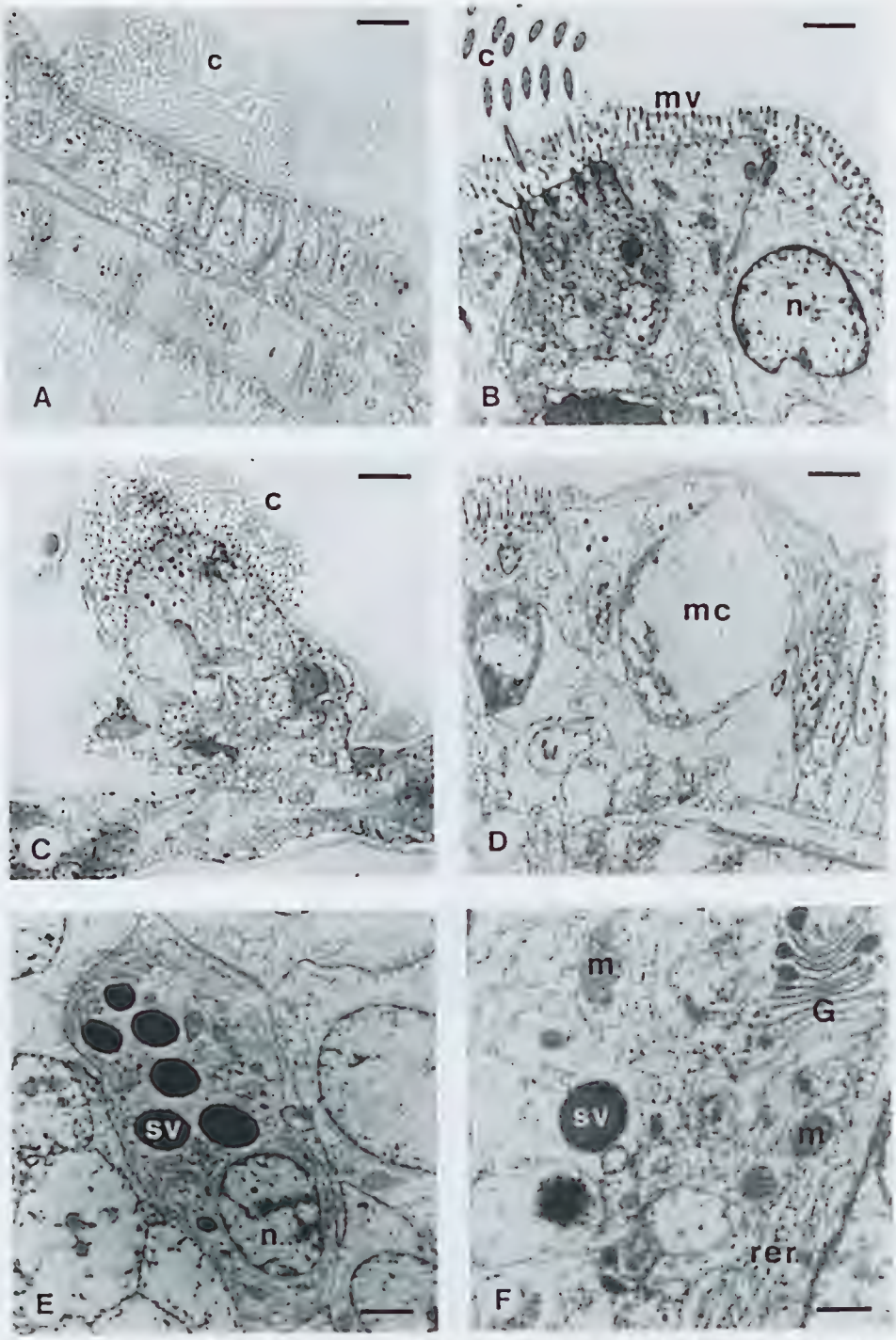

Plate 2. TEM micrographs of the gill of *Austrocochlea constricta*. A. Part of gill filament showing single layered epithelium. Bar = 10 µm. B. Ciliated and non-ciliated cells. Bar = 1 µm. C. Nodule. Bar = 7 µm. D. Mucous cell. Bar = 1.1 µm. E. Secretory cell. Bar = 1.2 µm. F. Detail of secretory cell. Bar = 0.4 µm. Key: b, basal bodies; c, cilia; G, Golgi apparatus; m, mitochondria; mc, mucous cell; mv, microvilli; n, nucleus; rer, rough endoplasmatic reticulum; sv, secretory vesicle.

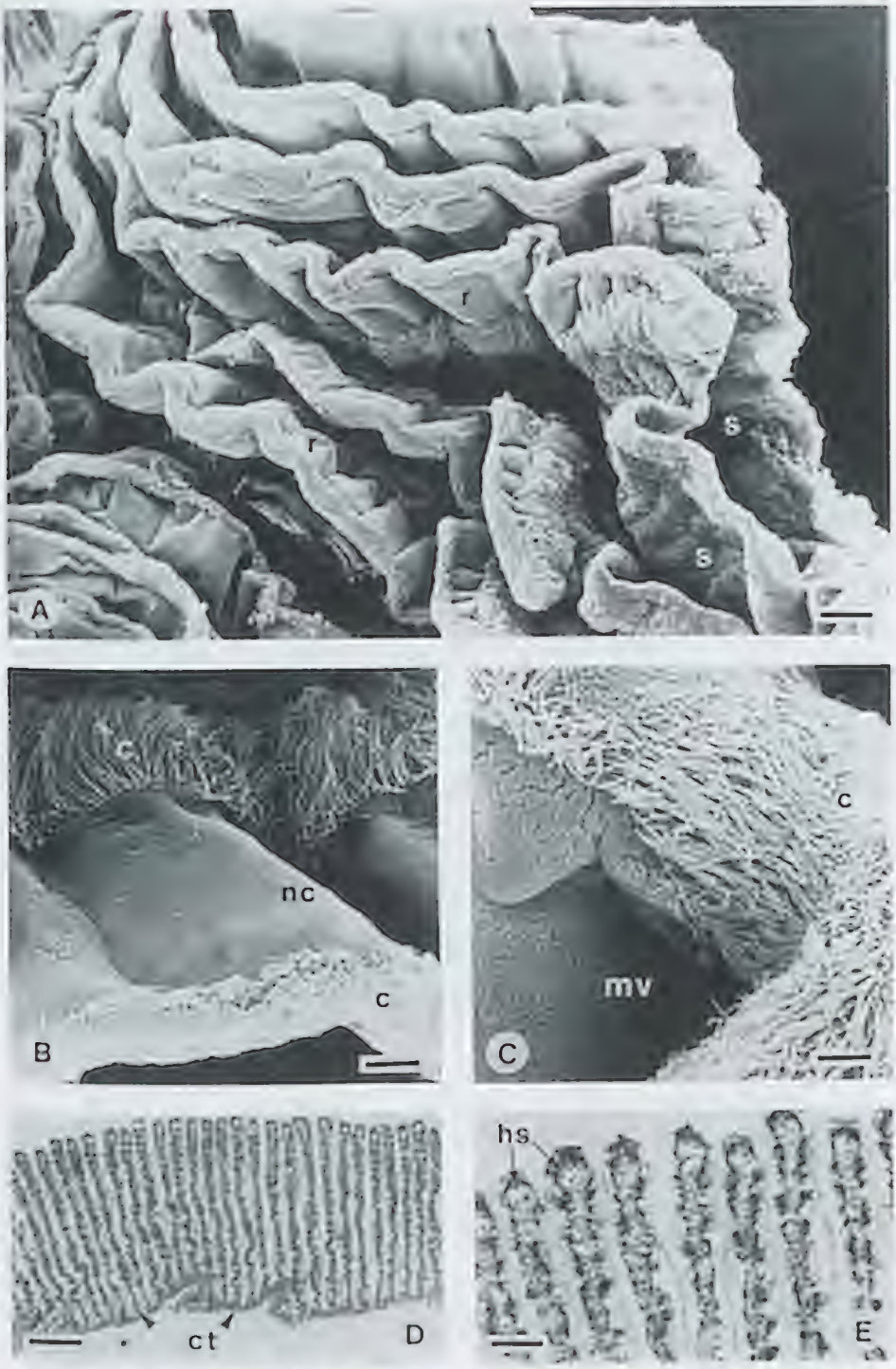

Plate 3 SEM and LM micrographs of the gill of *Planaxis sulcatus*. A. General dorsal view of gill filaments. Bar = 40 μm. B. Dorsal ridge of a filament. Bar = 13 μm. C. Detail of dorsal ridge. Bar = 4 μm. D. General view of the gill in LM section. Bar = 0.2 mm. E. Longitudinal section of filaments with haemocoelic spaces (hs). Bar = 60 μm. Key: r, dorsal ridge; s, thin sheet; c, cilia; nc, non-ciliated cells; mv, microvilli; ct, connective tissue.

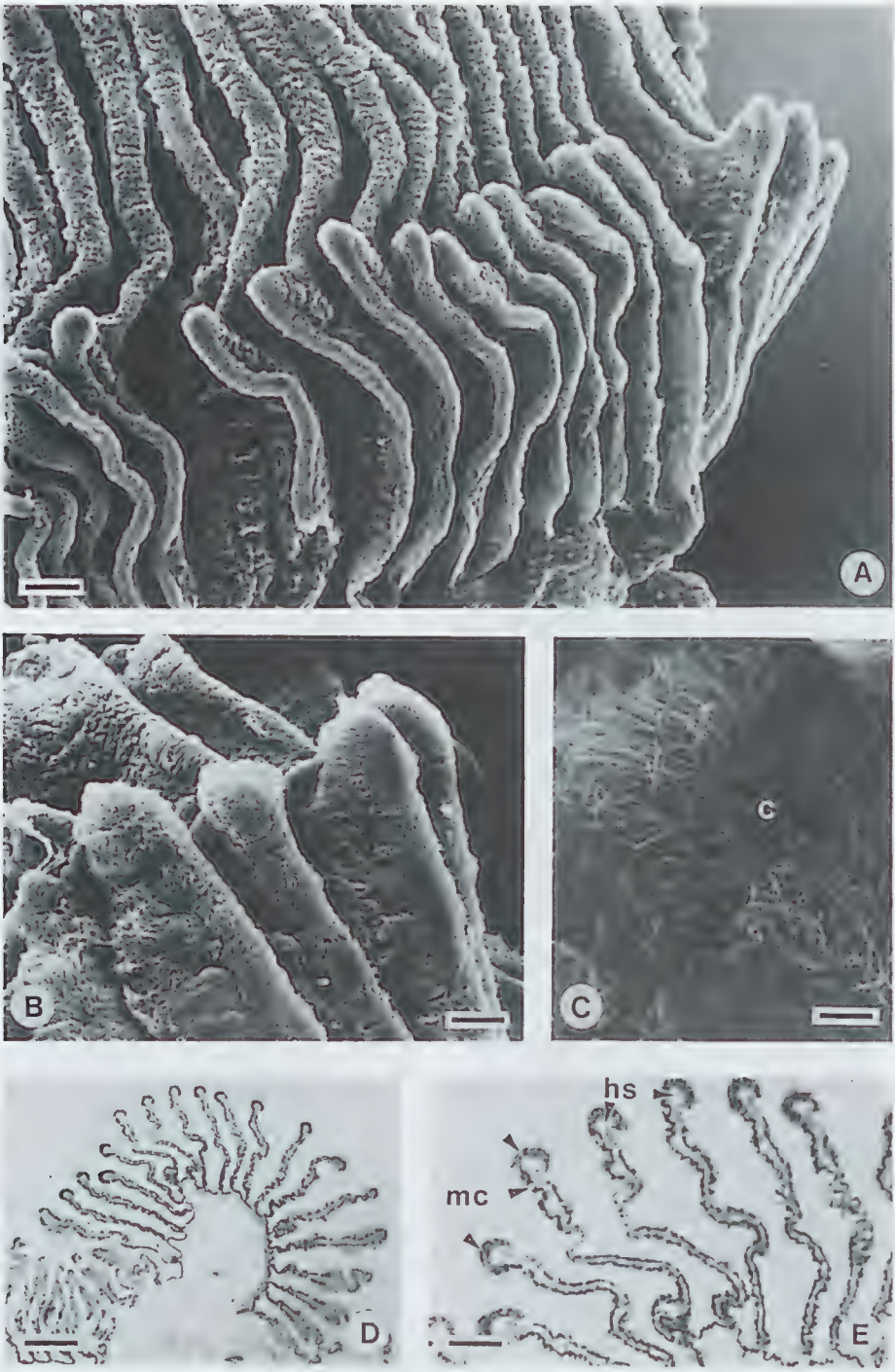

Plate 4. SEM and LM micrographs of the gill of *Littoraria articulata*. A. General dorsal view of the gill. Bar = 70 µm. B. Detail of a few filaments. Bar = 30 µm. C. Detail of one filament with border area between ciliated and non-ciliated cells. Bar = 2 µm. D. General view of the gill in LM section. Bar = 0.2 mm. E. Longitudinal section of filaments. Bar = 75 µm. Key: r, latero-dorsal ridge; s, thin sheet; c, cilia; mc, mucous cell; hs, haemocoelic space.

Plate 5 SEM and LM micrographs of the gill of *Bembicium auratum*. A. General lateral view of gill filaments. Bar = 40 µm. B. Detail of dorsal region of a gill filament. Bar = 20 µm. C. Detail of dorsal ridge. Bar = 13 µm. D. General view of the gill in LM section. Bar = 0.2 mm. E. Longitudinal section of gill filaments. Bar = 55 µm. Key: r, dorsal ridge; s, thin sheet, c, cilia; ct, connective tissue; mc, mucous cells.

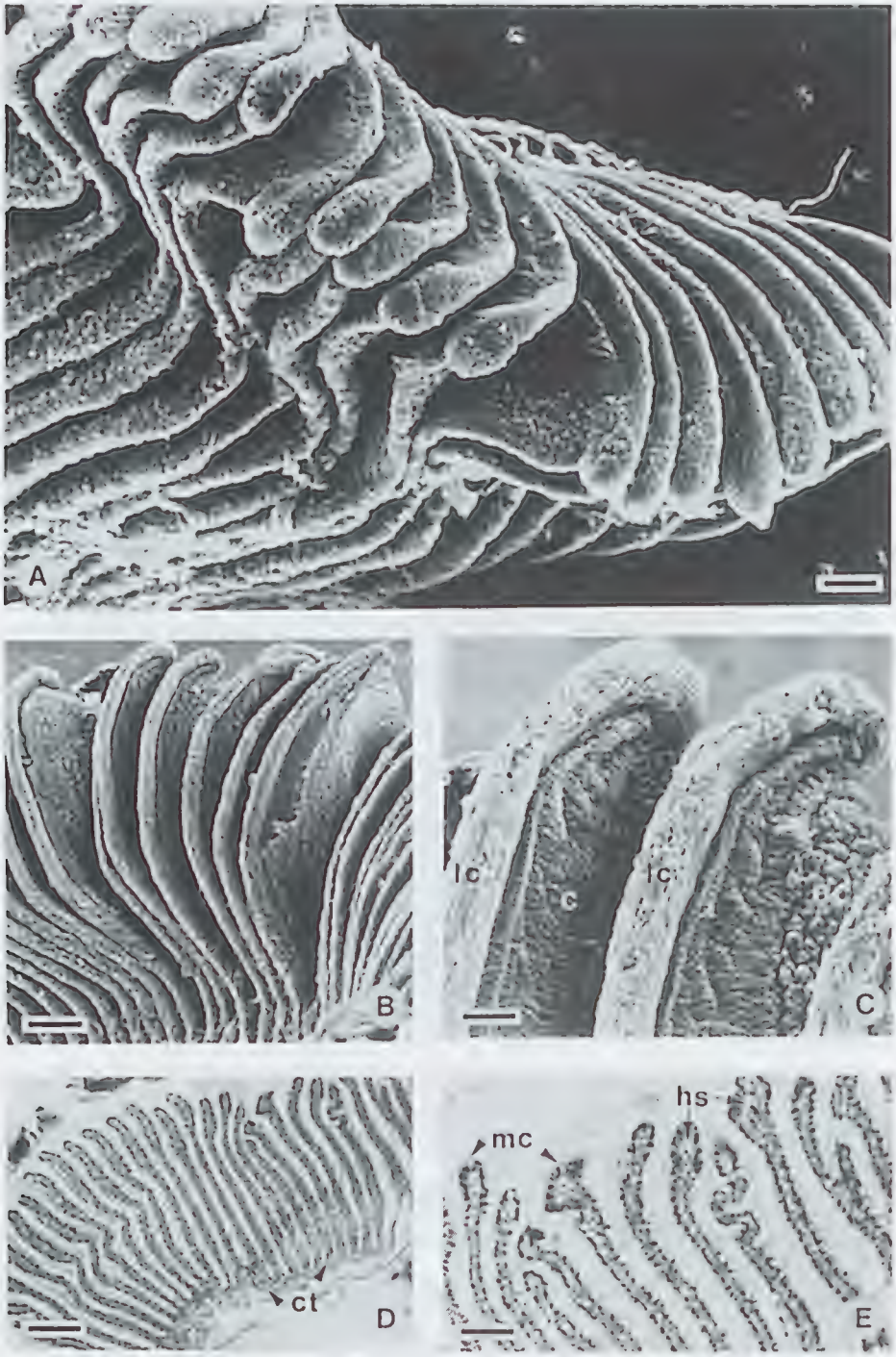

Plate 6. SEM and LM micrographs of the gill of *Mytilus marginalba*. A. General dorsal view of gill. Bar = 55 µm. B. Lateral view of a number of filaments. Bar = 0.14 mm. C. Detail of two filaments. Bar = 35 µm. D. General view of gill in LM section. Bar = 0.2 mm. E. Longitudinal section of gill filaments. Bar = 80 µm. Key: lc, long cilia; c, cilia; nc, non-ciliated cells; ct, connective tissue; mc, mucous cells; hs, haemocoelic space.

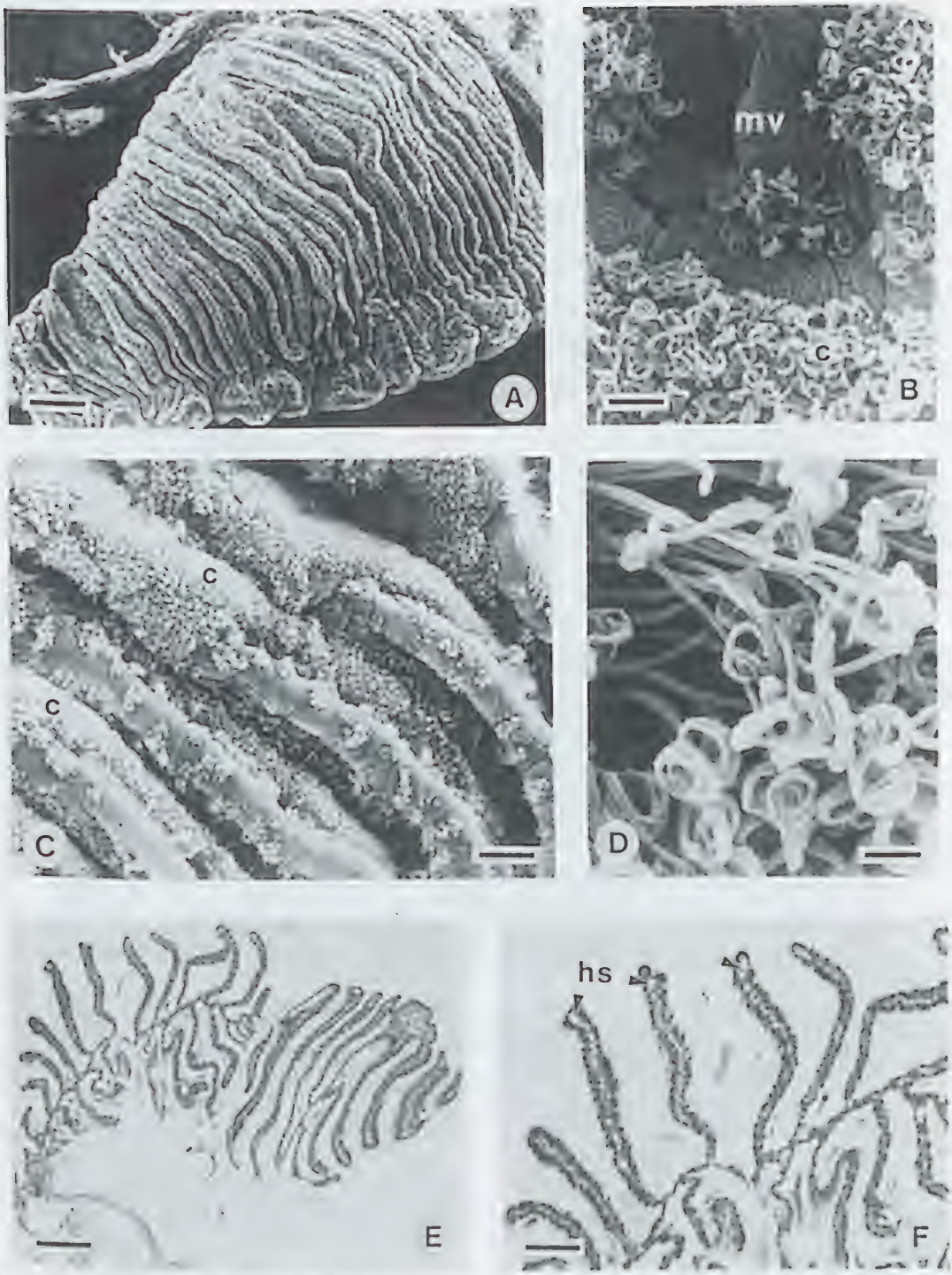

Plate 7 SEM and LM micrographs of the gill of *Patelloida mumula*. A. General dorsal view of the gill. Bar = 0.15 mm. B. Part of filament with ciliated and non-ciliated cells. Bar = 4 µm. C. Detail of a number of filaments. Bar = 25 µm. D. Paddle shaped cilia. Bar = 1 µm. E. General view of gill in LM section. Bar = 0.2 mm. F. Longitudinal section of gill filaments. Bar = 95 µm. Key: mv, microvilli; c, paddle shaped cilia; hs, haemocoelic space.

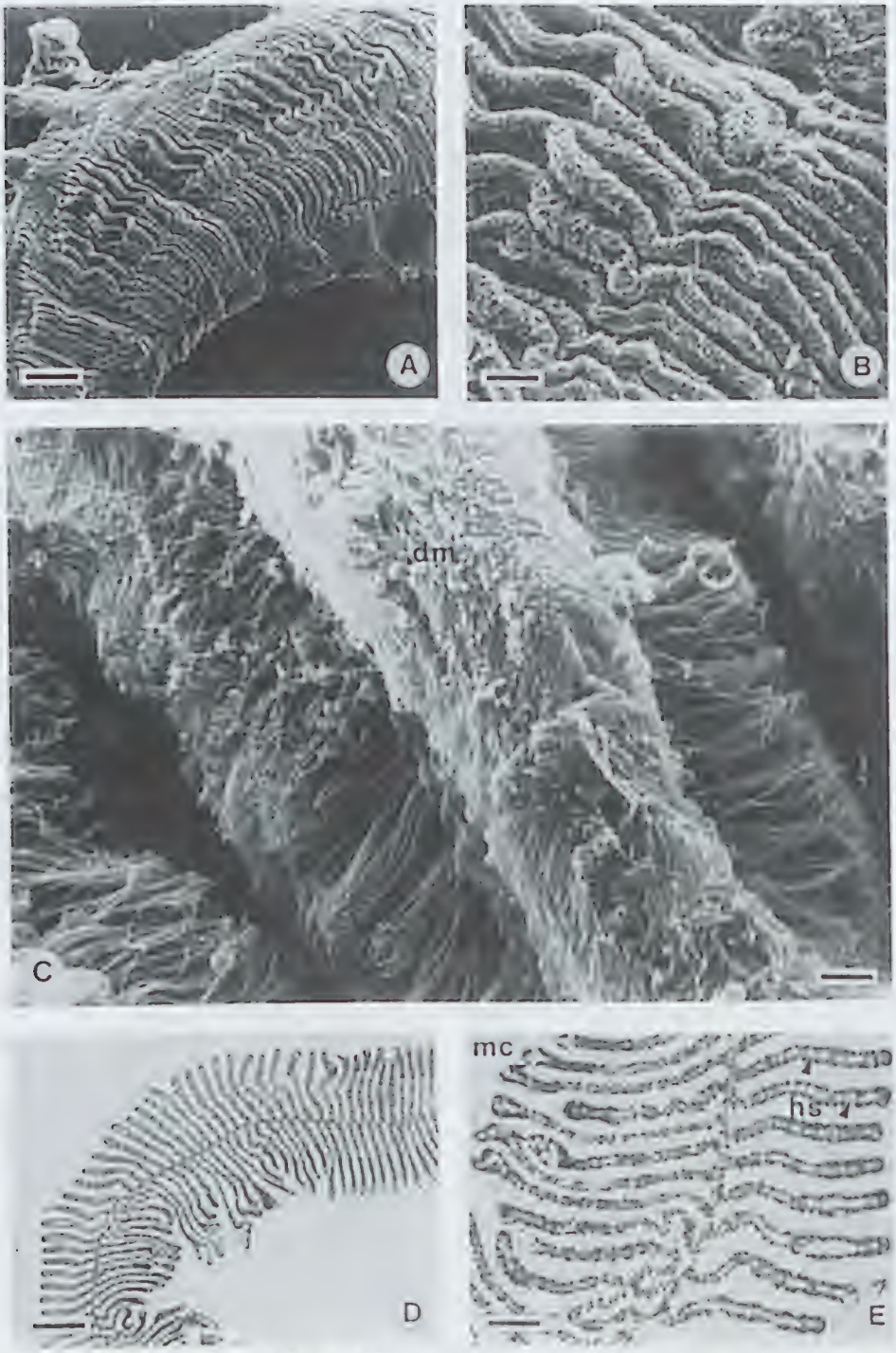

Plate 8. SEM and LM micrographs of the gill of *Nereis chamaeleon*. A. General dorsal view of the gill. Bar = 0.15 mm. B. Detail of a number of filaments. Bar = 55 µm. C. Detail of one filament. Bar = 0.5 mm. D. General view of gill in LM section. Bar = 0.15 mm. E. Longitudinal section of gill filaments. Bar = 55 µm. Key: dm, dorsal margin; mc, mucous cell; hs, haemocoelic space.

Planaxis sulcatus (Caenogastropoda, Planaxidae)

The caenogastropod *P. sulcatus* has a single monopectinate gill, positioned on the left side of the mantle cavity, attached to the mantle wall. The gill filaments extend from the anterior margin of the mantle deep into the mantle cavity. They are positioned parallel to each other and appear morphologically identical, although the size of the filaments gradually decreases posteriorly. Each filament has a narrow dorsal ridge, which extends ventrally as a thin sheet of tissue (Plate 3A). Each ridge is corrugated and covered at the margins with long cilia (Plate 3B). The central area of the ridge, consisting of non-ciliated cells, has a very smooth appearance and its surface is covered with microvilli (Plate 3C). The thin sheet of tissue extending from the dorsal ridge consists of non-ciliated cells and has a rougher appearance than the non-ciliated surface of the ridge (Plate 3A). Light microscopic sections confirm the parallel orientation of the gill filaments and show that the filaments are joined together at their base (Plate 3D). Haemocoelic spaces can be observed inside individual filaments (Plate 3E). Connective tissue, present inside the filaments and along the base where filaments fuse, presumably provides structural support. No secretory cells could be observed (Plate 3E).

Littoraria articulata (Caenogastropoda, Littorinidae, Littorininae)

In the caenogastropod *L. articulata*, a single monopectinate gill is present, positioned on the left side of the mantle cavity, and all gill filaments appear morphologically identical (Plate 4A). Each filament possesses a latero-dorsal ridge, which extends as a thin sheet of tissue across the mantle cavity. This gives each filament a somewhat triangular and elongated appearance (Plate 4B). The margins of the latero-dorsal ridge are covered with long cilia, while the cells of the elongated sheet are non-ciliated (Plate 4B + C). Light microscopic sections show that all filaments are linked to a common base (Plate 4D). In each filament a haemocoelic space is visible, forming a wider, round canal anteriorly inside the latero-dorsal ridge. Goblet type mucous cells are present in the anterior part of the filaments (Plate 4E).

Bembicium auratum (Caenogastropoda, Littorinidae, Lacuninae)

The single monopectinate gill of the caenogastropod *B. auratum* is attached to the mantle wall on the left side of the mantle cavity and consists of triangular shaped filaments (Plate 5A). All filaments appear uniform in shape, but from the anterior side onwards they gradually increase in size, and posteriorly a small reduction occurs. The dorsal surface of the filament is formed by a ridge showing numerous irregular folds (Plate 5C). The margins of the ridge consist of ciliated cells, surrounding a central area of non-ciliated cells, which has a rougher appearance than the corresponding area in *P. sulcatus*. The remaining part of the filament is formed by a thin sheet of tissue, composed of non-ciliated cells (Plate 5A + B). Light microscopic sections show that all filaments are joined together at the base, which is supported by connective tissue (Plate 5D). Each filament shows a haemocoelic space and anteriorly a well developed group of mucous cells (Plate 5E). It can also be clearly seen that although the filaments appear uniform in shape, they differ substantially in size.

Morula marginalba (Caenogastropoda, Muricidae)

The caenogastropod *M. marginalba* has a single monopectinate gill, positioned on the left side of the mantle cavity. The anterior part of the gill is not aligned with the mantle edge, but was observed more posteriorly in the mantle cavity. The gill filaments lie parallel to each other and are slightly curved (Plate 6A + B). The rounded dorsal ridge of each filament, extending from the base to the apex, is covered with long cilia. Adjacent to the ridge, a second area of ciliated cells is present, although these cilia are shorter than the previous ones (Plate 6C). The remaining part of the filament is formed by a sheet of tissue consisting of non-ciliated cells and has a rough appearance. Light microscopic sections reveal that the double layer of connective tissue present inside the gill filaments, not only encloses the haemocoelic space, but also extends into the base where filaments merge (Plate

6D). The widened anterior parts of the filaments, representing the rounded edges (Plate 6C), form the major haemolymph canals. Mucous cells, closely resembling goblet cells, can be observed in the anterior part of the filaments (Plate 6E).

Patelloida mimula (Patellogastropoda, Acmaeidae)

The gill of the acmaeid limpet *P. mimula* is triangularly shaped, pointing anteriorly (Plate 7A). It is positioned in the centre of the mantle cavity, extending forward to the mantle margin and attached to the mantle by a thin membrane. The individual filaments lie parallel to each other, are uniform in shape and increase in size posteriorly. Large areas of the filaments are covered by cilia, which differ from the ordinary type by the presence of terminal paddles (Plate 7B + D). The paddles appear to consist of a solid outer margin covered on one side by a thin membrane. Ciliated and non-ciliated cells are not organized in any recognizable pattern (Plate 7C). Large uninterrupted areas of ciliated cells are alternated with areas that consist largely of non-ciliated cells, but that include numerous small tufts of ciliated cells. Light microscopic sections show that the gill of *P. mimula* is not monopectinate, as it appears to be in SEM preparations, but bipectinate. All filaments join in the centre, although in an alternating rather than strictly paired fashion (Plate 7E + F). In the centre of each filament the haemocoelic space is visible. No secretory cells were observed.

Nerita chameleon (Neritimorpha, Neritidae)

The neritamorph *N. chameleon* has an elongated triangular shaped gill, positioned slightly left of centre in the mantle cavity and pointing anteriorly (Plate 8A). The gill is attached to the mantle by a thin membrane. All filaments lie parallel to each other and are corrugated (Plate 8B). The dorsal margin and lateral surfaces of each filament are covered with cilia. However, cilia associated with the lateral surfaces are longer, and orientated differently from those of the dorsal margin (Plate 8C). Light microscopic sections show that *N. chameleon* has a bipectinate gill, whose filaments are linked to a central base. The linkage is unpaired and the left and right filaments alternate. A haemocoelic space can be seen in the centre of each filament and towards the anterior end goblet type mucous cells were observed.

Discussion

External ultrastructure: The present study demonstrates pronounced differences in ctenidial morphology among the investigated gastropod species from Moreton Bay. The results show that species belonging to the clades Patellogastropoda (*P. mimula*), Neritimorpha (*N. chameleon*) and Vetigastropoda (*A. constricta*) possess bipectinate gills, whereas species belonging to the more advanced Caenogastropoda (*L. articulata*, *B. auratum*, *P. sulcatus* and *M. marginalba*) have monopectinate gills. The gills of Vetigastropoda, a group to which the trochid *A. constricta* belongs, are characterized by the presence of a skeletal rod, which has a supportive function. In *A. constricta* the gill filaments of the outer row are much shorter (1.1 ± 0.1 mm) than those of the inner row (3.2 ± 0.1 mm). This modification, which was observed also in other Trochoidea species and in the gills of the related vetigastropod family Lepetodriloidea, is considered to be a transitional condition from a bipectinate to a monopectinate gill structure (Haszprunar, 1988). Gill filaments covered with rows of nodules and regular patterns of ciliated and non-ciliated cells, as observed in *A. constricta*, have not been reported in ctenidia of other species. Randomly distributed clusters of cilia were observed on the lamellae of the secondary gills of the limpet *P. vulgata* (Nuwayhid *et al.*, 1978) and the pulmonate limpet *Siphonaria capensis* (De Villiers and Hodgson, 1987). However, from a taxonomic – phylogenetic perspective ctenidial structures cannot be compared to features of secondary gills, as these two types of gills are not homologous. Although there are three ciliated areas on the gill filaments of *A. constricta* (margin – nodules – striped pattern of ciliated cells), it is unclear as to what extent they function to generate water currents, disperse mucous and other gill secretions, or aid in cleansing of the gill filaments.

The lack of a skeletal rod in the bipectinate gills of the acmaeid limpet *P. mimula* and the neritid *N. chameleon* may be considered a primitive condition (Haszprunar, 1988). The gill structure of these representatives of the clades Patellogastropoda and Neritimorpha is remarkably similar. The gill of *P. mimula* is more distinctly triangular in shape in comparison to the gill of *N. chameleon*, but in both species the gill is positioned in the centre of the mantle cavity, the gill filaments lie parallel to each other and the linkage of the left and right filaments to the base is alternating.

The gills of the caenogastropod species *P. sulcatus*, *L. articulata*, *B. auratum* and *M. marginalba* have a basically uniform composition, although species specific variation occurs. Each gill filament consists of a clearly defined (latero-)dorsal ridge, which extends as a thin sheet of tissue across the mantle cavity. The shape of the filaments shows species specific differences. The gill filaments of the closely related littorinids *L. articulata* and *B. auratum* both appear triangular in shape, although the gill filaments of *L. articulata* are very much more elongated than those of *B. auratum*. The gill filaments of the muricid *M. marginalba* are slightly curved, giving the gills a quite distinct appearance. The gill filaments of the planaxid *P. sulcatus* are recognizable by the corrugated nature of the dorsal ridge, which may be a modification to enlarge the total gill surface area and improve respiratory gas exchange.

The gill filaments of all investigated species possessed areas of ciliated alternating with areas of non-ciliated cells. In general it can be stated that the main gill margin of all investigated species consisted of ciliated cells. In cases where the gill filaments possess a clearly defined ridge, as in the caenogastropods *P. sulcatus*, *L. articulata* and *B. auratum* and *M. marginalba*, both the dorsal and ventral margins of the ridge consist of ciliated cells. If present, the enclosed area of the ridge has a wavy appearance and is non-ciliated. The dorsal ridge of *M. marginalba* differs from this general pattern by not having a central area of non-ciliated cells. In this species the outer margin of the ridge is covered with long cilia, bordered by an area of cells that bear shorter cilia. The cilia were of the ordinary straight type with sharp terminals in all species except the acmaeid limpet *P. mimula*, where each cilium had a paddle shaped terminal. Similar cilia have been observed only in the secondary gills of the siphonariid limpet *S. capensis* (De Villiers and Hodgson, 1987), but not in the common patellid limpet *P. vulgata* (Nuwayhid *et al.*, 1978). Paddle shaped cilia have been reported to occur in molluscan osphradia, where they perform a chemoreceptive function (Haszprunar, 1985). However, De Villiers and Hodgson (1987) were unable to detect any nerve connections to these cilia in the pallial gills of *S. capensis* suggesting that their only function is as water paddles, as originally proposed by Yonge (1952). It has been demonstrated in *P. vulgata*, that movement of cilia creates a water current in the opposite direction to the haemolymph flow through the gill filaments, thus establishing a counter current mechanism for respiratory gas exchange (Nuwayhid *et al.*, 1978). The flattened tips of the cilia of *P. mimula* would be expected to magnify the strength of the water current, increasing the efficiency of the cilia as water paddles. Ciliary movement also takes part in distributing mucous secretions, that serve to capture foreign particles and remove them from the gills.

Internal structure: In terms of internal structure, gastropod gills are less disparate than their external ultrastructure suggests. Light microscopical sections showed that gill filaments of all species studied have a standard internal architecture. Whether gills were mono- or bipectinate, individual filaments showed basic similarities. All filaments were positioned parallel to each other and were linked by a common base, through which the haemolymph is directed and distributed to the individual filaments for respiratory gas exchange. Each filament consists of a unicellular epithelium, presumably to enhance a rapid gas exchange, and is supported by connective tissue which partly encloses the haemocoelic space. When comparing the ultrastructure of the gill epithelium of *A. constricta* with data from literature one should realise that most studies dealt with species that possess secondary gills. A single layered epithelium, consisting of either columnar or cuboidal cells, has been found in most species studied so far: *S. capensis* (De Villiers and Hodgson, 1987), *P. vulgata* (Nuwayhid *et al.*, 1978), the nudibranchs *Archidoris pseudoargus* and *Peltodoris atromaculata* (Jonas, 1986), the freshwater bivalve *Anodonta woodiana lauta* (Nakao, 1975). However, there appears to be a difference in the thickness of the epithelial cells,

which ranges from 4 µm for the cuboidal cells in the gill of *S. capensis* (De Villiers and Hodgson, 1987) to 10 – 50 µm for the columnar cells in the gills of the nudibranchs *A. pseudoargus* and *P. atromaculata* (Jonas, 1986). The columnar cells in the gill epithelium of *A. constricta* have an average thickness of 13.8 µm, which is similar to the thickness of the columnar cells in the bivalve *Lucina costata* (Giere, 1985). De Villiers and Hodgson (1987) suggested that there is a direct relationship between the thickness of epithelial cells and the degree of protection. Unprotected gills would be prone to desiccation and therefore would need to have thicker epithelial cells. This may be the case for some species, but the present results do not support this theory. Although the columnar cells in the gills of *A. constricta* could be classed as being moderately thick, the gill itself is located inside the mantle cavity and therefore is well protected from any desiccating influence.

Mucous secreting cells were observed in all species except *P. sulcatus* and *P. mimula*. They were usually of the ordinary goblet type except in the littorinid *B. auratum*, where the mucous cells were larger and were grouped in the anterior region of the filament. The presence of mucous cells and other secretory cells in gill filaments is not uniform throughout molluscan species. In the gills of the common limpet *P. vulgata* (Nuwayhid *et al.*, 1978) and the freshwater bivalve *A. woodiana lauta* (Nakao, 1975), mucous cells or other secretory cells were not observed. Jonas (1986), however, located three types of granular gland cells and an additional mucous cell in nudibranchs. The TEM study into the internal gill ultrastructure of *A. constricta* showed that the goblet type mucous cells contain one mucus-filled vacuole and, like the surrounding epithelial cells, possess microvilli. The structure of the mucous cells is comparable to those described previously. The second type of secretory cell observed in the gill of *A. constricta* has not been reported in any other molluscan gill. Large membrane bound secretions are present throughout the cell. Since this cell is found totally enclosed by other cells or bordering the filament surface, it is unclear whether the secretory products are secreted externally, or into the haemolymph or both. Further cytochemical study is certainly needed to clarify the functioning of this cell type. De Villiers and Hodgson (1987) suggested that the possession of mucous cells may be related to gill location. Exposed gills, as observed in the pulmonate *S. capensis*, in contrast to internal gills would not need mucous cells, as ciliary currents would be adequate to keep the lamellae clear of debris. The gills of all investigated species in this study are well protected inside the mantle cavity and the absence of mucous cells in *P. sulcatus* and *P. mimula* does not agree with Hodgson's suggestion. The presence or absence of mucous cells does not seem to be related directly to the habitat of the investigated species, as mucous cells were observed in species inhabiting the shore at low to mid tidal level (*A. constricta*, *M. marginalba*) as well as in species inhabiting the shore at high tidal level (*L. articulata*) (Eertman & Hailstone, 1988).

Concluding, it can be said that apparent species specific differences in external gill ultrastructure do not imply functional differences between gills. Each species has developed its own gill morphology presumably to optimize respiratory gas exchange. Features that characterize gill

Table 2. A summary of the features that characterize the ctenidia of the investigated gastropods.

Species	Clade	Type of gill	Uniform rows of filaments	Clearly defined dorsal ridge	Skeletal rod/ nodules	Shape of filaments	Paddle shaped cilia	Secretory cells
A. constricta	Vetigastropda	bipectinate	–	–	+	blade	–	+
P. mimula	Patellogastropoda	bipectinate	+	–	–	*	+	–
N. chameleon	Neritimorpha	bipectinate	+	–	–	*	–	+
P. sulcatus	Caenogastropoda	monopectinate		+	–	corrugated	–	–
L. articulata	Caenogastropoda	monopectinate		+	–	triangular	–	+
B. auratum	Caenogastropoda	monopectinate		+	–	triangular	–	+
M. marginalba	Caenogastropoda	monopectinate		+	–	curved	–	+

* Individual filaments do not have a characteristic shape.

morphology of the investigated species are summarized in Table 2. The external ultrastructure of the investigated caenogastropod species showed basic uniformity, as did the gills of the limpet *P. mimula* and neritid *N. chameleon*, representatives of the Patellogastropoda and Neritimorpha respectively. The gill ultrastructure of the vetigastropod trochid *A. constricta* showed the least similarities with the ultrastructure of the gills of the other species investigated.

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Two new species of *Amalda* from the Saya de Malha Bank (Gastropoda: Olividae: Ancillinae)

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Amalda danilai and *A. trippneri* n. spp. are described from the Saya de Malha Bank, between Mauritius and the Seychelles.

Key words: Taxonomy, Olividae, Ancillinae, *Amalda*, Mascarene Ridge.

Introduction

The Saya de Malha Bank forms part of the Mascarene Ridge, a narrow plateau that extends approximately from Mauritius to the Seychelles. Although little is known about its molluscan fauna, its benthos was extensively sampled by a succession of Russian expeditions between 1962 and 1989 (see Bondarev & Röckel (1992) for a general account). Prior to this, the only published report on the molluscs was that of Melvill (1909), based on a few samples taken in 1905 by the Percy Sladen Trust Expedition. Since these expeditions, papers have appeared on species of Volutidae (Bouchet & Bail, 1991), Cassidae (Abbott, 1993) and Conidae (Röckel & Korn, 1990).

Amongst the more conspicuous new species dredged by the Russian expeditions are several Olividae of the subfamily Ancillinae, specimens of which, from the collection of Mr Henrikas Danila of Lithuania, have been sent to me by Dr Axel Alf of Ludwigsburg, Germany. There are described below.

Terminology in the description follows Kilburn (1977).

Taxonomy

Genus *Amalda* H. & A. Adams, 1853

Amalda danilai n. sp.

Pl. 1, figs 1–2

Ancilla sp.; Bondarev & Röckel 1992: 30, colour fig. 1 (p. 31).

Description: Shell oblong-ovate-fusiform with moderately broad base, breadth/length 0.43–0.45, body whorl more or less evenly convex on both sides, greatest width of shell more or less median, aperture moderately large, aperture length/total length 0.48–0.52; spire cyrtoconoid with somewhat mamillate apex, spire angle about 44° , apical angle about 58° . Primary callus thick and enveloping entire spire except for protoconch, deeply impressed at final suture, surface of callus glossy, not microshagreened, but with 6 strong spiral ridges; secondary callus forms a pad covering entire right side of spire, with a narrow anterior extension reaching the false umbilicus. Aperture lanceolate, very bluntly rounded posteriorly, widest at about middle; outer lip in side view straight, very slightly prosocline, with a very blunt basal denticle; siphonal notch moderately deep, narrowly and asymmetrically U-shaped. Columellar pillar strongly twisted, its termination acute, with a very deep, inverted L-shaped basal notch; pleats 2–4, the innermost only slightly weaker than others, outermost separated by a slightly wider groove; microshagreen sculpture not visible. Anterior fasciolar groove fairly wide and deep for genus, continuing posteriorly to form a shallow false umbilicus posterior to

Plate 1. *Amalda danilai* and *Amalda trippneri* n. spp. 1–2, holotype of *A. danilai*, Natal Museum L1606/T979, dimensions 34.4 x 15.1 mm. 3–4, holotype of *A. trippneri*, Natal Museum L1607/T980, dimensions 53.8 x 19.6 mm.

midline of inner lip; inner lip evenly concave anteriorly, in parietal region becoming convex with 5 weak transverse pleats. Anterior fasciolar band convex, posterior fasciolar band flattened and slightly declivous, its posterior margin raised prominently above ancillid band and delimited by a deep furrow; ancillid groove moderately deep, its band very slightly rounded and declivous; median zone with fine growth lines only. Number of teleoconch whorls indeterminate.

Protoconch conically-domed, of about 2,5 whorls (limit not clear), protoconch 1 small and depressed; breadth about 1.7 mm.

Median zone greyish-white; callus deposits pure white, except for a deep brownish-orange blotch encircling apex (but not colouring protoconch), and a pale buff zone below suture of body whorl dorsally and a faint buff tinge on adjacent spire callus.

Dimensions: 34.4 x 15.1 mm, aperture 17.3 mm (holotype); largest paratype 44.6 x 22.7 mm.

Type material: Holotype Natal Museum L1606/T979, don H. Danila. Three paratypes in collection H. Danila.

Type locality: Saya de Malha Bank. 1989, No other details are provided, but the holotype may be from the sample for which Bondarev & Röckel (1992) give the depth as 60 m.

Notes: In shape and spire characters, *Amalda danilai* would appear to be a typical member of subgenus *Alocospira* Cossmann, 1899, yet the development of a false umbilicus, albeit slight, could also be interpreted as associating it with the genus *Eburna* Lamarck, 1801. Indeed Voskuil (1991), in a review of that genus, regarded *Amalda* as a subgenus of *Eburna*, although proposing that the former should be restricted to western hemisphere species. A possible sister species to *A. danilai* is *Ancilla nitida* Wanner & Hahn, 1935, from the lower Miocene of Java, which has a similar coarsely grooved spire callus, deeply notched columella base and a false umbilicus that is even more deeply perforate. Treating the distinct false umbilicus as apomorphic, Kilburn (1981) suggested that *nitida* could be regarded as an Indo-Pacific representative of *Eburna*. However, it is more likely that the development of a false umbilicus is convergent, and both *nitida* and *danilai* are here referred to *Amalda s.l.*.

Amalda nitida differs from *A. danilai* in its much deeper false umbilicus, spirally grooved posterior fasciolar band and more strongly furrowed spire callus. Of Recent species, *A. danilai* shows closest similarity to *Amalda mamillata* (Hinds, 1844) of the South China Sea, which differs in having more numerous spiral ridges and stronger microshagreen sculpture on the spire, a non-mamillate apex, shallower columella notch, no false umbilicus and different coloration.

Etymology: Named in honour of Mr Henrikas Danila.

Amalda trippneri sp. n.

Pl. 1, figs 3–4

Ancilla rubiginosa (*non* Swainson, 1825); Melvill 1909: 113.

Ancilla sp; Bondarev & Röckel 1992: 30, colour figs 2–3 (p. 31).

Description: Shell fusiform with moderately broad base, breadth/length 0.36–0.39, body whorl gently and more or less evenly convex on both sides, greatest width of shell anterior to median, aperture length/total length 0.44–0.45; spire narrowly cyrtoconoid with blunt apex, spire angle 31°–35°. Primary spire callus thick and enveloping entire spire except for protoconch 1, only slightly impressed at suture, surface of callus glossy, not microshagreened, but with spiral ridges more or less visible under surface, not apparent in relief, except sometimes for about 5 lirae on 1st teleoconch whorl and 1–3 above suture on penultimate whorl; secondary callus forms a pad covering right side of spire from 2nd teleoconch whorl on, with a narrow anterior extension reaching posterior fasciolar

band. Aperture somewhat lanceolate, but obliquely truncate posteriorly, widest anterior to middle, outer lip in side view very shallowly sigmoid and very slightly prosocline, with two very blunt basal denticles, one on each side of termination of posterior fasciolar band; siphonal notch moderate, broadly and asymmetrically U-shaped. Columella pillar strongly twisted, its termination acute, with a very deep, inverted L-shaped basal notch; pleats 4–6, the innermost weak, outermost separated by a slightly wider and deeper groove; microshagreen sculpture not visible. Anterior fasciolar groove fairly deep and wide for genus, continuing posteriorly to form a very slight false umbilicus at midline of inner lip; inner lip shallowly concave anteriorly, apart from a slight convexity anterior to level of false umbilicus; parietal region weakly convex with faint traces of several transverse pleats. Anterior and posterior fasciolar bands each flattened to concave, moderately declivous, posterior margin raised prominently above ancillid band and delimited by a furrow; ancillid groove moderately deep, its band very slightly rounded, either level with median zone or sunken; median zone with fine growth lines only. Number of teleoconch whorls probably about 5.

Protoconch limits not clear, protoconch 1 flattened.

Median zone pale buff to cream; posterior band darker (deep to pale buff), spire callus deposit tinged with orange-buff or yellow.

Dimensions: 53.8 x 19.6 mm (holotype); 62.7 x 24.4 mm (larger paratype).

Type material: Holotype Natal Museum L1607/T980, don. H. Danila. Two paratypes in collection H. Danila.

Type locality: Saya de Malha Bank, 1989.

Plate 2. *Amalda rubiginosa* (Swainson, 1825): holotype of *Ancillaria rubiginosa*, Natural History Museum, London, 19785, dimensions 68.4 x 27.5 mm, "China".

Notes: *Amalda trippneri* belongs to the *A. hilgendorfi* species-complex (see Kilburn & Bouchet 1988: 285). It is closest in appearance to *Amalda rubiginosa* (Swainson, 1825) and *A. hilgendorfi* (von Martens, 1897). Indeed, *A. trippneri* is doubtlessly the species recorded from the Saya de Malha Bank in 150 fathoms by Melvill (1909) as *Ancilla rubiginosa*, although the actual specimen ("one broken shell") cannot now be traced (it is not in the Melvill collection (National Museum of Wales), nor in that of the Natural History Museum, London). The true *Amalda rubiginosa* (Pl. 2) has a lower spire than *A. trippneri* (aperture length/total length 0.50–0.54, spire angle 39°–47°, n = 14), a sharper apex with the entire protoconch exposed, and fine microshagreen sculpture on the secondary callus. It should be noted that the correct name for the *Baryspira rubiginosa* of modern authors is *Amalda albocallosa* (Lischke, 1873), and that the true habitat of the very different *A. rubiginosa* remains uncertain. All specimens examined by me originate from 19th century collections, and most are labelled "China" (the type locality), which is restricted to "Hong Kong" in the case of two examples from the Lombe-Taylor collection, housed in the Natural History Museum (London). This locality may prove to be correct, as the holotype of *Amalda* (*Alocospira*) *hayashii* Ninomiya (1988: 145, pl. 1, figs 7–8) from Amami-Oshima, southern Japan, is very possibly based on an immature individual of *A. rubiginosa*.

Amalda hilgendorfi, a form or subspecies of which occurs off Madagascar, lacks spiral lirae on the spire, the spire callus is distinctly microshagreened, the ancillid groove is barely impressed and the anterior fasciolar band bears a median ridge.

Etymology: At Dr Alf's request I have named this species in honour of Mr Edmund Trippner, well known among German collectors for his helpfulness and generosity.

Acknowledgements

I am indebted to Mr Henrikas Danila and Dr Axel Alf for sending me this material. I thank Dr John Taylor of the Natural History Museum (London) for permitting me to study material in that collection, and Ms Kathie Way for sending photographs of the holotype of *Ancillaria rubiginosa*. Mrs Linda Davis helped in the preparation of plates, and Drs D.G. Herbert and A. Alf kindly read the manuscript.

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Book review

Bouchet, P. (Editor). 1995. Résultats des Campagnes MUSORSTOM. Volume 14. Mémoirs du Muséum National d'Histoire Naturelle, Paris. Volume 167: 1-654. ISBN 2-85653-217-9. 600 French francs plus postage. Available from: Dr W Backhuys, PO Box 321, 2300 AH Leiden, The Netherlands.

During the 1980s the Múseum National d'Histoire Naturelle in Paris conducted an ambitious sampling program in the oceanic waters off New Caledonia and other areas of the Pacific and Indian Oceans, such as the Chesterfield Islands in the Coral Sea, Philippines, Indonesia, and the southwestern Indian Ocean. Sample sites ranged from intertidal and shallow subtidal work in the lagoons to depths of several hundred metres or more on the slopes and on into the oceanic depths. Collecting samples was only the first, small part of the work. The material was then sent to France and sorted into the various major animal groups, then resorted to species, an extremely laborious process. Specialists in particular groups from throughout the world have been strongly encouraged to research the systematics of the various taxa. In many cases funding has been provided to allow researchers to work on the material at the Paris Museum for some months where they have had access to all the specimens and at the same time the library and other resources of a major museum.

As proof of the success of the program, the present volume is the fourteenth in the series of *Résultats des Campagnes MUSORSTOM*, and the second on molluscs. There are 10 papers by a total of 15 authors in this volume which present new results on the taxonomy, classification and biogeography of the Bivalvia (Pectinoidea, *Meiocardia,* Glossidae, Trapeziidae, and Anomalodesmata), Scaphopoda, and Gastropoda (Calliostomatidae, Trophoninae, Volutidae, Drilliidae, Conidae, and Mathildidae). The comprehensive MUSORSTOM sampling in deep waters has resulted in the discovery of a wealth of new taxa in a wide variety of animal groups, including molluscs.

The present volume alone contains descriptions of 1 new subfamily, 9 new genera and 142 new species. The scaphopod section by Victor Scarabino is the largest paper in the volume. It discusses 139 species, 42 of which are new (in addition there are three new genera). A revised classification of all scaphopods is proposed which recognises 44 genera worldwide. The radulae of 42 of these genera are figured. The calliostomatid paper by Bruce Marshall describes 27 new species, 4 new genera, a new tribe, and raises the Calliostomatidae to full family status. Roland Houart describes 2 new genera and 24 new species of Trophoninae. My own paper on drilliids describes 22 new species. All except one of the remaining papers also contain new taxa.

The papers are of high quality by recognised experts in the groups studied. Presentation is good with clear illustrations and a standard formatting for all papers. The 654 pages contain a wealth of information about Indo-Pacific molluscs.

Volume 14 of *Résultats des Campagnes MUSORSTOM* (and the preceding Volume 7, also on molluscs) are essential additions to the library of anyone interested in Indo-Pacific molluscs. Dr Philippe Bouchet, the volume editor, is to be sincerely congratulated for his energetic work in obtaining the material, encouraging researchers to work it up, and his fine efforts in seeing the volume through to final publication.

There are many groups which have not yet been studied, and we can look forward to a future volume in the series containing much more information developed from this energetic program.

Fred E Wells

Moll. Res. 17: 27–48 (1996).

Callista, Lioconcha and *Pitar* in New Caledonia and adjacent waters (Mollusca, Veneridae)

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Key words: Mollusca, Veneridae, New Caledonia, distribution, new species

Abstract

Three species of *Callista,* seven species of *Lioconcha* including two undescribed species, *Lioconcha melharteae* sp. nov. and *Lioconcha richerdeforgesi* sp. nov., and twelve species of *Pitar* including a previously undescribed species, *Pitar healyi* sp. nov., are recorded from material collected in the waters off New Caledonia.

Introduction

The waters of New Caledonia and surrounding areas provide within a relatively small area, a wide variety of underwater habitats comprising lagoons, reef slopes, seamounts and guyots, a sedimentary basin, trenches and volcanoes. This area is broadly defined as the New Caledonian economic zone (Richer de Forges 1990). For the past 10 years this area has been the focus of extensive sampling programmes conducted by the ORSTOM Institute, New Caledonia, aimed at documenting its diverse marine fauna. A full narrative of these cruises, including comprehensive station lists detailing latitude, longitude, depth, habitat type and collecting method, have been published elsewhere (Richer de Forges 1990, 1991) and are not repeated here. This study details the diversity and distribution of the venerid bivalves belonging to *Callista, Lioconcha* and *Pitar* based upon material collected on these expeditions. A small amount of material from the collection of J. Vidal has also been included. All material used in this study is housed in the Museum National d'Histoire Naturelle, Paris (MNHN). Although lacking registration numbers, the expedition material is uniquely identified by the combination of cruise name and station number.

Abbreviations used: lv, left valve; rv, right valve; pv, paired valves.

Systematics

Family Veneridae Rafinesque, 1815

Callista (Callista) accincta Römer, 1866

(Figure 1a–b)

Callista accincta Römer, 1866: 63, sp.19; pl.19, fig.1a, b.

Diagnosis: Shell moderately compressed, smooth, glossy, length to 60 mm. Sculpture of fine

concentric ridges and irregular growth pauses, ridges stronger marginally. Colour cream, orange or olive green, white umbonally, usually with two brown radial rays, white internally.

Material examined: Plateau des Chesterfield: (Corail 2: stn DW60, 1rv; stn DW110, 1rv; stn DW137, 1rv, 1pv, 110 m; stn DW82, 1rv). Bancs Lansdowne-Fairway: (Corail 2: stn DW21, 2pv, 86 m; stn CP27, 2pv, 74–75 m; stn DW04, 3lv, 1rv; stn CP24, 2rv; stn DW01, 1rv; stn DW02, 3rv, 2lv; stn DW08, 1rv, 1lv; stn DW18, 1pv, 69 m; stn DW09, 1rv. Chalcal 1: stn D9, 1lv). Nouvelle-Caledonie: Secteur de Noumea (Lagon: stn 290, 1pv, 11 m); Ile Ouen-Baie du Prony (Lagon: stn 129, 1pv, 1rv, 44–55 m); Grand Recif Sud (Lagon: stn 294, 1pv, 21 m; stn 311, 1pv, 36 m; stn 324, 1lv, 39 m; stn 334, 1pv, 47 m; stn 344, 1pv, 37 m; stn 383, 1rv, 62 m. Lagon: stn 545, 1pv, 37 m; stn 548, 1pv, 32 m; stn 555, 1pv, 55 m; stn 559, 1pv, 52 m; stn 560, 1pv, 48 m; stn 574, 1rv); Atoll de Huon (Lagon: stn 433, 1rv); Secteur de Yate (Lagon: stn 620, 1pv, 1rv, 50–52 m; stn 624, 1pv, 46–44 m; stn 641, 1rv); Secteur de Canala (Lagon: stn 696, 1rv; stn 697, 1pv, 1rv, 1lv, 57–41 m; stn 702, 1rv; stn 708, 1rv, 1lv; stn 724, 1rv; stn 725, 1pv, 2lv, 43 m; stn 729, 1pv, 42–45 m; stn 753, 1lv); Secteur de Thio (Lagon: stn 680, 1pv, 1rv, 33 m; stn 693, 2pv, 35–38 m;) Secteur de Poindimie (Lagon: stn 762, 1pv, 1lv, 43 m; stn 763, 1pv, 1lv, 42 m; stn 772, 3pv, 1lv, 30 m; stn 780, 1pv, 33 m; stn 800, 6pv, 33 m; stn 801, 2rv; stn 808, 1pv, 30 m); Grand Recif Mengalia (Lagon: stn 855, 1lv; stn 867, 1rv); Secteur de Poum (Lagon: stn 1026, 3pv, 29 m); Secteur de Belep (Lagon: stn 1154, 2lv, 1rv; stn 1156, 2rv, 2lv; stn 1157, 1pv, 3rv, 4lv, 55 m; stn 1159, 1rv, 1lv; stn 1063, 6lv, 1rv).

Remarks: The holotype of *Callista accincta* cannot be traced and the assignment of material to *C. accincta* is based on Römer's excellent illustrations. Most of the Römer types were contained in the Dohrn collection which was housed in the Stettin Museum. This institution was totally destroyed during World War II (Dance 1986: 210).

Callista (Callista) roseotincta (Smith, 1885)

(Figure 1c–d)

Cytherea roseotincta Smith, 1885: 136, pl.1, fig.6a, b.

Callista (Striacallista) roseotincta (Smith); Lamprell and Whitehead, 1992: sp.535.

Diagnosis: Shell thin, smooth, glossy, length to 23 mm. Colour white, blotched and radially rayed with fawn or pink; interior white, sometimes with the external pink rays visible internally.

Material examined: Nouvelle-Caledonie: Secteur de Noumea (Lagon: stn 8, 2pv, 15 m); Ile Ouen-Baie du Prony (Lagon: stn 64, 1pv, 15 m; stn 66, 3pv, 15 m; stn 80, 1pv, 33 m; stn 83, 1pv, 22 m; stn 120, 1pv, 46 m. Lagon: stn 226, 20pv, 22 m; stn 239, 1pv, 43 m); Baie de St Vincent (Lagon: stn 170, 2pv, 22 m); Grand Recif Sud (Lagon: stn 293, 6pv, 20 m; stn 296, 1pv, 26 m; stn 304, 1pv, 27 m; stn 308, 2pv, 18 m; stn 311, 1pv, 1lv, 36 m; stn 312, 1pv, 26 m; stn 313, 1pv, 30 m; stn 324, 2pv, 1rv, 2lv, 39 m; stn 334, 1pv, 2rv, 2lv, 47 m; stn 339, 1pv, 26 m; stn 340, 3pv, 1lv, 27 m; stn 344, 1pv, 37 m; stn 345, 1pv, 39 m; stn 367, 1pv, 105 m; stn 377, 1rv; stn 386, 2lv, 1rv; stn 405, 1pv, 27 m; stn 544, 2pv, 1lv, 25 m; stn 547, 4pv, 29 m; stn 548, 2pv, 33 m); Ile de Pins (Lagon: stn 581, 3pv; stn 589, 2pv, 1rv, 1lv, 31 m; stn 590, 1pv, 20 m; stn 591, 2pv, 16 m; stn 596, 2pv, 35 m); Atoll de Surprise (Lagon: stn 473, 1pv, 50 m); Secteur de Yate (Lagon: stn 632, 4pv, 2rv, 45 m; stn 644, 1pv, 48–45 m); Secteur de Thio (Lagon: stn 675, 1pv, 43 m; stn 680, 1pv, 33 m; stn 681, 1pv, 33 m; stn 682, 5pv, 37 m); Secteur de Canala (Lagon: stn 696, 1pv, 57–41 m; stn 701, 1pv, 39 m; stn 702, 3pv, 37 m; stn 703, 2pv, 40 m; stn 707, 1pv, 38 m; stn 725, 2pv, 1rv, 43 m; stn 730, 6pv, 43 m; stn 731, 1pv, 42 m; stn 754, 1pv, 36 m); Secteur de Poindimie (Lagon: stn 771, 1pv, 34 m; stn 772, 1pv, 30 m; stn 780, 1pv, 33 m; stn 781, 2pv, 36 m); Grand Recif Mengalia (Lagon: stn 867, 1rv); Secteur de Pouebo (Lagon: stn 892, 1pv, 26 m; stn 894, 1rv); Secteur de Poum (Lagon: stn 984, 1pv, 23 m; stn 991, 1pv; stn 995, 1rv; stn 1015, 2pv, 25 m; stn 1016, 1pv, 20 m; stn 1025, 2 pv, 28 m); Secteur de Balabio (Lagon: stn 1046, 1pv, 7 m); Secteur des Belep (Lagon: stn 1157, 1rv; stn 1168, 1lv, 1rv).

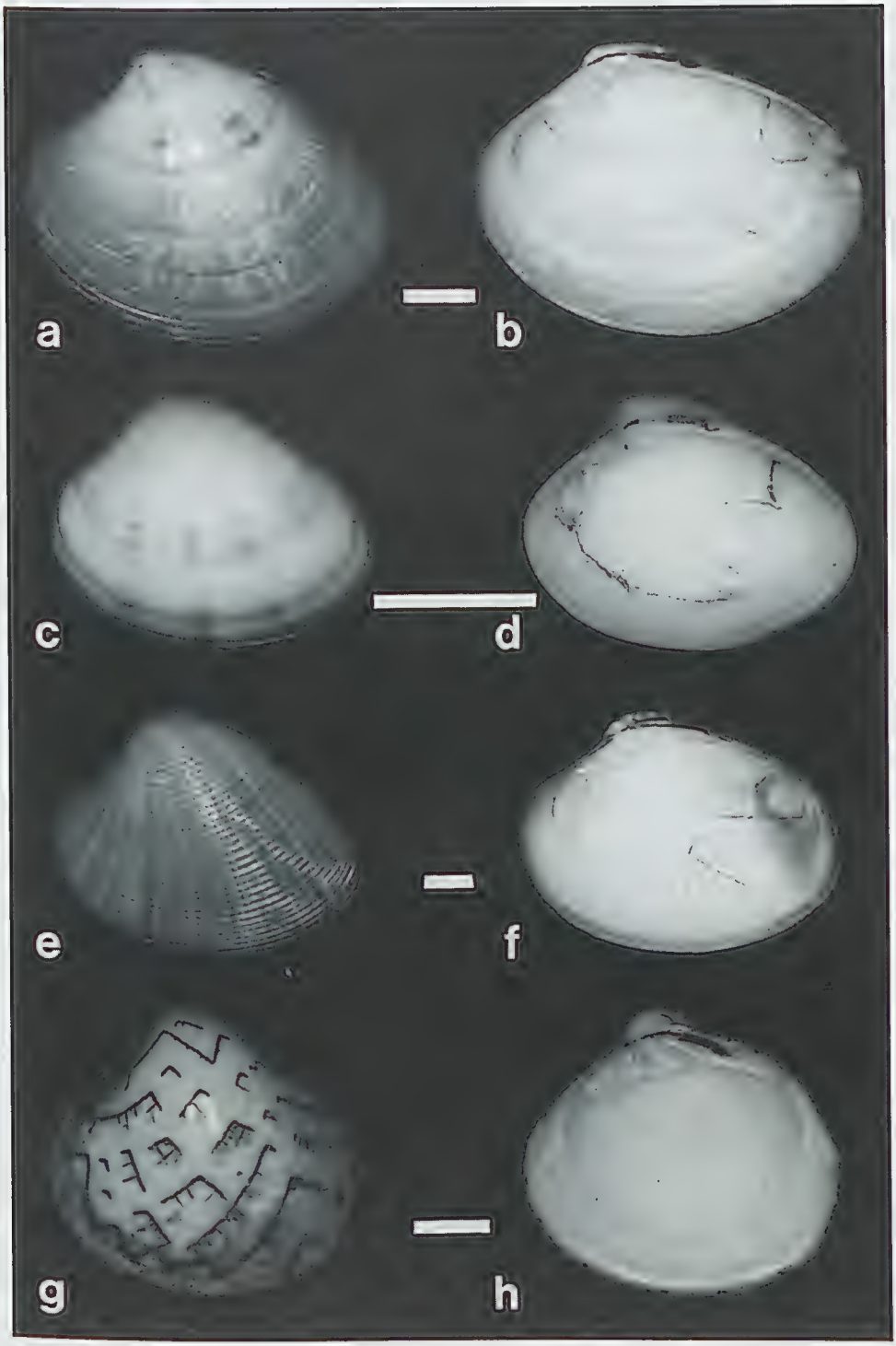

Figure 1. a–b. *Callista (Callista) accincta* Römer, Corail 2: stn DW21; c–d. *Callista (C.) roseotincta* (Smith), Lagon: stn 226; e–f. *Callista (Costacallista) lilacina* (Lamarck), Lagon: stn 1024; g–h. *Lioconcha (Lioconcha) castrensis* (Linnaeus), Musorstom: stn DW431. Scale bars equal 10 mm.

Ride des Loyaute: (SMIB 5: stn DW81, 2rv, 1lv; stn DW92, 1pv, 110 m).

Remarks: Smith (1885) described *C. roseotincta* from one right valve in which the anterior cardinal tooth was missing. A description of the teeth from an intact specimen is as follows:–left valve anterior lateral strong, peg-like; anterior cardinal thin, almost wafer-like, slightly concave joined at apex to posterior cardinal, separated from it by a deep socket; posterior cardinal thick at base, slightly concave; posterior lateral thin, moderately short, parallel to escutcheon; right valve anterior lateral pit deep; anterior cardinal strong, thin edged, separated by a deep slit from the posterior cardinal; posterior cardinal thick with deep pit separating it from the posterior lateral; posterior lateral thick. In addition Smith (1885), referred to 2 internal broad radial rose-pink rays towards the upper part of the valve. However, many of the specimens examined were white internally.

Callista (Costacallista) lilacina (Lamarck, 1818)

(Figure 1e–f)

Cytherea lilacina Lamarck, 1818: 302, fig.15.

Cytherea pectoralis Sowerby, 1853: 625, pl.130, fig.75; non Lamarck, 1818.

Dione grata Deshayes, 1853: 62.

Callista (Costacallista) lilacina (Lamarck); Lamprell and Whitehead 1992: sp.537.

Diagnosis: Shell solid, length to 75 mm. Sculpture of close-set, narrow, concentric ridges. Colour brown, with slightly darker brown radial rays, purple-brown at the margins posteriorly and the lunule; interior white, centrally and at hinge, with purple margins.

Material examined: Nouvelle-Caledonie: Secteur de Pouebo (Lagon: stn 895, 5pv, 16 m; stn 901, 1pv, 1rv, 22–40 m; stn 903, 1rv); Secteur de Koumac (Lagon: stn 931, 1pv, 21 m); Secteur de Poum (Lagon: stn 1024, 1pv, 1rv, 1lv, 26 m; stn 1029, 1lv); Secteur de Balabio (Lagon: stn 1056, 1pv, 22 m); Secteur des Belep (Lagon: stn 1069, 1pv, 2rv, 1lv, 30 m; stn 1095, 1rv; stn 1117, 2pv, 36 m; stn 1129, 4pv, 40 m).

Remarks: These New Caledonian records of *C. lilacina* are from the northern limit of the species' Indo-Pacific range. The absence of this species from the Chesterfield Plateau is surprising.

Lioconcha (Lioconcha) castrensis (Linnaeus, 1758)

(Figure 1g–h)

Venus castrensis Linnaeus, 1758: 1132.

Cytherea ornata Lamarck, 1818: 309; non Dillwyn, 1817.

Lioconcha (Lioconcha) castrensis (Linnaeus); Lamprell and Whitehead 1992: sp.543.

Diagnosis: Shell solid, length to 50 mm. Colour variable, usually white, with chevron patterns varying from blue-black to tan; some Great Barrier Reef shells have hieroglyphic patterns; interior white or pale orange.

Material examined: Plateau des Chesterfield: (Corail 2: stn DW46, 4pv, 1lv, 21 m; stn DW50, 1lv; stn DW51, 1pv, 69 m; stn DW69, 1pv, 30–52 m; stn DW87, 1rv, 1lv; stn DW97, 1lv; stn DW136, 1pv, 1rv, 37 m; stn DW138, 1rv, 1lv; stn DW148, 1pv, 1rv, 148 m). Bancs Lansdowne-Fairway: (Corail 2: stn DW10, 1lv. Chalcal 1: stn D7, 2lv; stn D24, 1rv; stn D62, 1rv). Plateau Chesterfield-Bellona (Chalcal 1: stn CP16, 1lv; stn 39, 1pv, 4lv, 3rv, 63 m; stn D55, 1pv, 23 m; stn D61, 1lv). Nouvelle-Caledonie: Secteur de Noumea (Lagon: stn 34, 1rv. Lagon: stn 284, 1lv); Ile Ouen-Baie du

Prony (Lagon: stn 98, 2pv, 39 m); Baie de St Vincent (Lagon: stn 214, 1pv, 12 m; stn 218, 1rv); Grand Recif Sud (Lagon: stn 293, 6pv, 20 m; stn 305, 1pv, 1lv, 26 m; stn 308, 1pv, 18 m; stn 312, 2pv, 26 m; stn 340, 4pv, 27 m; stn 344, 3pv, 37 m; stn 544, 1pv, 1lv, 25 m; stn 546, 1pv, 33 m); Atoll de Surprise (Lagon: stn 461, 1pv, 35 m; stn 466, 1pv, 42 m; stn 473, 1pv, 50 m); Lagon Nord (Lagon: stn 480, 1pv, 1rv, 31 m; stn 487, 3pv, 37 m; stn 489, 1lv; stn 521, 1pv, 39 m); Ile de Pins (Lagon: stn 589, 3pv, 31 m; stn 594, 1pv, 27 m); Secteur de Thio (Lagon: stn 677, 1pv, 32 m); Grand Recif Mengalia (Lagon: stn 853, 1pv, 27 m; stn 866, 1pv, 26 m); Secteur de Koumac (Lagon: stn 917, 1pv, 27 m); Secteur de Poum (Lagon: stn 1006, 1pv, 25 m; stn 1016, 1pv, 20 m;) Secteur des Belep (Lagon: stn 1145, 1rv; stn 1159, 2pv, 50 m; stn 1182, 1lv; stn 1189, 1rv). Ride des Loyaute: (Musorstom 6: stn DW431, 1pv, 21 m).

Remarks: *Lioconcha castrensis* is very variable in size, shape and colour and can easily be confused with *L. ornata, L. annettae* and *L. fastigiata* which have a similar tented, colour pattern. However, compared with these species *L. castrensis* is larger in size and has a more ovate shape.

Lioconcha (Lioconcha) polita (Röding, 1798)
(Figure 2a–b)

Venus polita Röding, 1798: 181.

Cytherea sulcatina Lamarck, 1818: 568.

Lioconcha (Lioconcha) polita (Röding); Lamprell and Whitehead, 1992: sp.547.

Diagnosis: Shell solid, inflated, length to 30 mm. Colour dark brown or orange with concentric chevron or zigzaging patterns and rays; interior white, dark red-purple posteriorly, often ventrally; usually yellow centrally.

Material examined: Plateau Chesterfield-Bellona: (Chalcal 1: stn D44, 5pv, 38 m). Nouvelle-Caledonie: Secteur de Noumea (Lagon: stn CP1, 1pv, 70 m; stn 11, 4pv, 24 m; stn 33, 1rv; stn 43, 1pv, 25 m; stn 54, 1pv, 25 m; stn 55, 2pv, 23 m; stn 58, 8pv, 22 m; stn 263, 1pv, 23 m; stn 264, 2pv, 19 m; stn 268, 1pv, 24 m; stn 271, 1pv, 22 m; stn 274, 3pv, 12 m; stn 280, 1pv, 24 m; stn 286, 1pv, 28 m); Ile Ouen-Baie du Prony (Lagon: stn 85, 1pv, 21 m; stn 104, 2pv, 24 m; stn 157, 1pv, 15 m); Baie de St Vincent (Lagon: stn 165, 1pv, 21 m; stn 166, 1pv, 10 m; stn 167, 2pv, 11 m; stn 168, 5pv, 10 m; stn 179, 1pv, 12 m; stn 181, 1pv, 10 m; stn 197, 3pv, 6 m; stn 198, 1pv, 14 m; stn 203, 5pv, 1rv, 1lv, 13 m; stn 205, 1rv, 1lv; stn 209, 2pv, 1rv, 14 m; stn 211, 1pv, 12 m; stn 215, 2pv, 14 m; stn 216, 3pv, 1rv, 1lv, 14 m); Grand Recif Sud (Lagon: stn 404, 1lv; stn 405, 3pv, 1rv, 27 m; stn 406, 1lv); Atoll de Huon (Lagon: stn 438, 1pv, 37 m; stn 439, 84pv, 39 m); Atoll de Surprise (Lagon: stn 447, 3pv, 1rv, 36 m; stn 448, 1pv, 30 m; stn 451, 1rv; stn 455, 1pv, 40 m; stn 456, 2pv, 1rv, 37 m; stn 466, 3pv, 1rv, 42 m; stn 469, 2pv, 2rv, 1lv, 39 m; stn 471, 2pv, 42 m); Ile de Pins (Lagon: stn 596, 2pv, 35 m; stn 581, 2pv, 23 m; stn 595, 2pv, 1rv, 37 m; stn 590, 1rv); Secteur de Pouebo (Lagon: stn 892, 1pv, 26 m; stn 895, 1pv, 16 m); Secteur de Koumac (Lagon: stn 905, 1pv, 57 m; stn 932, 5pv, 1rv, 23 m; stn 944, 1pv, 15 m; stn 945, 1pv, 16 m; stn 950, 3pv, 13 m; stn 953, 2pv, 1rv, 19 m; stn 956, 1pv, 17 m); Secteur de Poum (Lagon: stn 962, 6pv, 26 m; stn 971, 6pv, 1rv, 26 m; stn 973, 1pv, 27 m; stn 989, 3pv, 21 m; stn 990, 1pv, 23 m; stn 996, 1lv; stn 998, 1rv; stn 999, 1pv, 22 m; stn 1004, 3pv, 15 m; stn 1005, 5pv, 17 m; stn 1008, 1pv, 27 m; stn 1009, 2pv, 20 m; stn 1010, 2pv, 16 m; stn 1012, 3pv, 15 m; stn 1011, 3pv, 14 m; stn 1013, 1pv, 18 m; stn 1018, 1pv, 21 m; stn 1025, 1pv, 28 m; stn 1035, 2pv, 15 m; stn 1037, 2pv, 25 m); Secteur de Balabio (Lagon: stn 1039, 2pv, 21 m; stn 1056, 2pv, 1rv, 22 m); Secteur des Belep (Lagon: stn 1065, 3rv, 2lv; stn 1067, 6rv, 2lv; stn 1069, 6pv, 30 m; stn 1070, 1pv, 2lv, 29 m; stn 1071, 1pv, 1rv, 26 m; stn 1073, 3lv, 3rv; stn 1075, 2lv; stn 1076, 11rv, 6lv; stn 1077, 2rv; stn 1078, 1lv; stn 1079, 5lv, 1rv; stn 1080, 2pv, 1lv, 1rv, 34 m; stn 1081, 6lv, 2rv, ; stn 1082, 5lv, 3rv; stn 1083; 2rv, 1lv; stn 1084, 3rv, 4lv; stn 1085, 4lv, 3rv; stn 1086, 4pv, 5lv, 6rv, 31 m; stn 1087, 3rv, 2lv; stn 1089, 4pv, 4rv, 3lv, 35 m; stn 1091,

1rv, 1lv; stn 1092, 2rv, 1lv; stn 1093, 1lv; stn 1095, 2pv, 29 m; stn 1097, 2rv; stn 1110, 2pv, 31 m; stn 1101, 1pv, 1lv, 38 m; stn 1102, 3pv, 38 m; stn 1103, 1pv, 5lv, 5rv, 32 m; stn 1106, 4pv, 39 m; stn 1108, 1pv, 40 m; stn 1109, 2pv, 2lv, 38 m; stn 1112, 4pv, 42 m; stn 1114, 1rv; stn 1115, 1pv, 42 m; stn 1121, 1rv; stn 1128, 1pv, 26 m; stn 1188, 1pv, 33 m; stn 1209, 2pv, 21 m; stn 1211, 1rv; stn 1212, 1pv, 22 m; stn 1214, 7pv, 1lv, 1rv, 29 m; stn 1216, 1pv, 30 m; stn 1217, 1rv).

Remarks: *Lioconcha polita* is well represented in the offshore waters of New Caledonia but like *Callista roseotincta* is, with a single exception, absent from the Chesterfield Plateau.

Lioconcha (Lioconcha) annettae Lamprell and Whitehead, 1990

(Figure 2c–d)

Lioconcha annettae Lamprell and Whitehead, 1990: 49, fig.4e–h; Lamprell and Whitehead, 1992: sp.545.

Diagnosis: Shell with umbones inflated, similar to *L. ornata* in shape, length to 38 mm. Colour white, with black, chestnut-red or dark-brown chevron or hieroglyphic patterns; interior white, yellow centrally.

Material examined: Plateau des Chesterfield (Corail 2: stn DW41, 1rv; stn DW46, 1rv; stn DW50, 4pv, 1lv, 2rv, 49 m; stn DW51, 2lv; stn DW60, 2lv, 1rv; stn DW61, 1rv; stn DW73, 1pv, 1lv, 240 m; stn DW82, 1lv; stn DW87, 6lv, 3pv, 31 m; stn DW126, 1lv, 1rv; stn DW128, 1pv, 3lv, 3rv, 38 m; stn DW147, 4pv, 25 m). Nouvelle-Caledonie: Baie de St vincent (Lagon: stn 214, 1pv, 1lv, 12 m); Ile Ouen-Baie du Prony (Lagon: stn 225, 1pv, 15 m); Secteur de Noumea (Lagon: stn 275, 1pv, 19 m); Grand Recif Sud (Lagon: stn 305, 2pv, 26 m; stn 341, 1pv, 19 m); Ile de Pins (Lagon: stn 590, 3pv, 20 m; stn 593, 3pv, 25 m); Grand Recif Mengalia (Lagon: stn 855, 2pv, 22 m); Secteur de Pouebo (Lagon: stn 888, 1lv). Ride des Loyaute: (Musorstom 6: stn DW432, 1pv, 1lv, 21 m; stn DW435, 2rv).

Remarks: *Lioconcha annettae* is more attenuate posteriorly than *L. ornata*. Internally *L. annettae* has a sub-umbonal, orange-yellow colour patch, whereas *L. ornata* has a central, yellow colour patch. A comprehensive study of the *annettae – ornata* complex may yet show these forms to be conspecific.

Lioconcha (Lioconcha) ornata (Dillwyn, 1817)

(Figure 2e–f)

Venus ornata Dillwyn, 1817: 184.

Cytherea picta Lamarck, 1818: 309.

Lioconcha (Lioconcha) ornata (Dillwyn); Lamprell and Whitehead, 1992: sp.544.

Diagnosis: Shell solid, umbones inflated, length to 50 mm. Colour usually cream, mostly with fine, dense, brown or black reticulate, chevron patterns and fine dots; interior white, yellow-orange centrally.

Material examined: Plateau des Chesterfield (Corail 2: stn DW31, 1pv, 10lv, 15rv, 57 m; stn DW32, 1pv, 11lv, 1rv, 55 m; stn DW33, 1pv, 52 m; stn DW34, 1pv, 47 m; stn DW38, 4pv, 61 m; stn DW40, 1pv, 2rv, 58 m; stn DW41, 4lv, 2rv; stn DW42, 4pv, 7lv, 7rv, 45 m; stn DW44, 2lv, 2rv; stn DW48, 4pv, 1lv, 44 m; stn DW50, 1pv, 49 m; stn DW51, 2pv, 69 m; stn DW59, 1pv, 1lv, 50 m; stn DW60, 1pv, 4lv, 4rv, 45 m; stn DW65, 2pv, 1rv, 62 m; stn DW67, 1rv; stn DW70, 1pv, 1rv, 54 m; stn DW72, 7pv, 2rv, 3lv, 32 m; stn DW76, 1pv, 2rv, 3lv, 53 m; stn DW77, 1lv, 1rv; stn DW80, 1rv; stn DW84, 1rv; stn DW85, 1rv; stn DW87, 1rv, 3pv, 31 m; stn DW88, 1pv, 20lv, 17rv, 32 m; stn

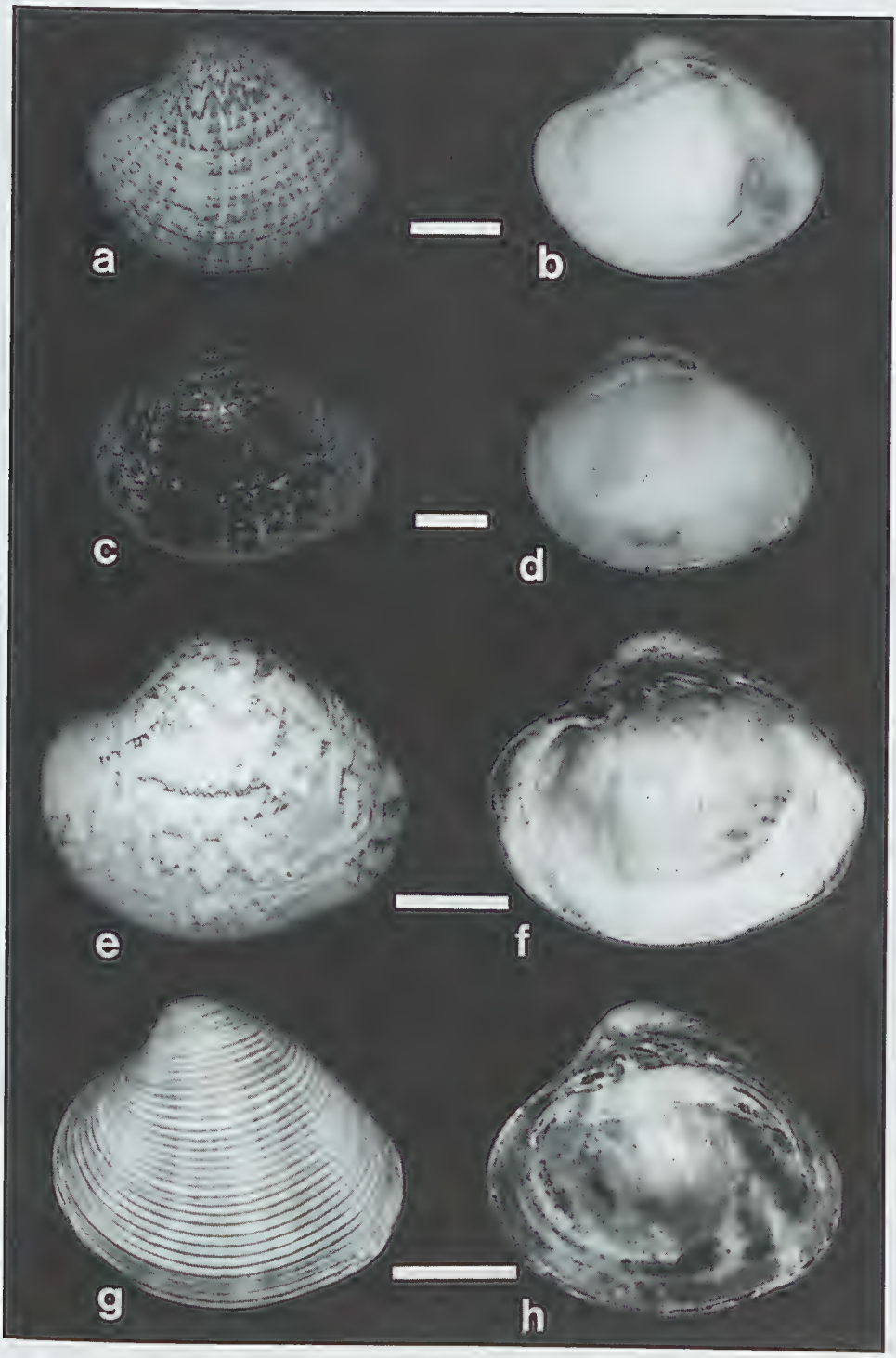

Figure 2. a–b. *Lioconcha (Lioconcha) polita* (Röding), Lagon: stn 1081; c–d. *Lioconcha (L.) annettae* Lamprell and Whitehead, Lagon: stn 275; e–f. *Lioconcha (L.) ornata* (Dillwyn), Lagon: stn 800; g–h. *Lioconcha (Sulcilioconcha) philippinarum* (Hanley), Lagon: stn 839. Scale bars equal 10 mm.

DW91, 3pv, 43 m; stn DW94, 3pv, 2rv, 36–53 m; stn DW96, 3pv, 1rv, 41 m; stn DW100, 1pv, 40 m; stn DW102, 1pv, 58 m; stn DW103, 1rv, 1lv; stn DW104, 1pv, 49 m; stn DW106, 1pv, 1lv, 62 m; stn DW110, 3pv, 2rv, 4lv, 40 m; stn DW116, 1rv; stn DW117, 1pv, 20 m; stn DW118, 2lv; stn DW121, 1pv, 3rv, 2lv, 12 m; stn DW122, 3pv, 1lv, 28 m; stn DW126, 2pv, 1lv, 19 m; stn DW128, 2rv; stn DW133, many; stn DW137, 2pv, 1lv, 37 m; stn DW138, 1rv; stn DW143, 1pv, 1rv, 32 m; stn DW145, 4pv, 1rv, 2lv, 15–30 m; stn DW146, 1lv, 1pv, 40–52 m; stn DW153, 1lv, 1rv; stn DW154, 1pv, 29 m; stn DW154, 2rv; stn DW155, 1pv, 1rv, 23 m; stn DW156, 2pv, 21 m; stn DW160, 1lv, 1rv; stn DW163, 1rv, 1lv; stn DW166, 1pv, 1rv, 10 m). Plateau Chesterfield-Bellona: (Chalcal 1: stn D17, 1pv, 8lv, 7rv, 44 m; stn D18, 2rv; stn D24, 1pv, 38 m; stn D26, 1pv, 1 rv, 1lv, 48 m; stn D28, 2lv; stn D39, 2pv, 40 m; stn D42, 1lv; stn D45, 4pv, 1 rv, 50 m; stn D47, 1pv, 70 m; stn D49, 1pv, 48 m; stn D54, 1pv, 36–42 m; stn D56, 1pv, 60 m; stn D60, 1pv, 3lv, 1rv, 45 m; stn D61, 1pv, 1lv, 50 m). Bancs Lansdowne-Fairway (Corail 2: stn DW18, 1pv, 1lv, 69 m; stn CP24, 1pv, 74–75 m). Nouvelle-Caledonie: Secteur de Noumea (Lagon: stn 1, 5pv, 19 m; stn 4, 5pv, 9 m; stn 8, 1pv, 15 m; stn 21, 2pv, 10 m; stn 22, 1lv; stn 27, 5pv, 2rv, 2lv, 18 m; stn 30, 1pv, 24 m; stn 41, 1pv, 28–46 m; stn 45, 1pv, 14 m; stn 49, 2pv, 10 m; stn 50, 4pv, 12 m; stn 51, 2pv, 10 m; stn 251, 3pv, 20 m; stn 257, 1pv, 9 m; stn 265, 1rv; stn 268, 1lv; stn 270, 3pv, 1lv, 25 m; stn 271, 2pv, 22 m; stn 272, 2pv, 22 m; stn 273, 1pv, 9 m; stn 274, 3pv, 12 m; stn 276, 3pv, 26 m; stn 277, 1pv, 30 m; stn 287, 2pv, 29 m; stn 289, 1pv, 23 m); Ile Ouen-Baie du Prony (Lagon: stn 64, 1pv, 15 m; stn 65, 5pv, 24 m; stn 66, 1pv, 15 m; stn 73, 2pv, 15 m; stn 77, 1pv, 22 m; stn 79, 1pv, 16 m; stn 80, 1pv, 33 m; stn 82, 5pv, 10 m; stn 83, 1pv, 22 m; stn 84, 3pv, 17 m; stn 89, 1pv, 32 m; stn 90, 1pv, 32 m; stn 93, 4pv, 17 m; stn 94, 3pv, 17 m; stn 95, 5pv, 14 m; stn 98, 4pv, 15 m; stn 99, 1pv, 14 m; stn 161, 1pv, 1rv, 20 m; stn 224, 2pv, 30 m; stn 226, 9pv, 28 m; stn 229, 1pv, 41 m; stn 233, 6pv, 30 m); Baie de St vincent (Lagon: stn 162, 2pv, 1rv, 10 m; stn 163, 1pv, 15 m; stn 168, 1pv, 10 m; stn 170, 1pv, 22 m; stn 173, 1pv, 20–50 m; stn 178, 2pv, 20 m; stn 180, 3pv, 10 m; stn 182, 1pv, 8 m; stn 186, 1pv, 1lv, 1rv, 11 m; stn 200, 1pv, 18 m; stn 201, 1pv; stn 206, 1pv; stn 214, 1pv, 1lv, 12 m; stn 217, 2pv, 1rv, 16 m; Grand Recif Sud (Lagon: stn 293, 7pv, 1rv, 20 m; stn 294, 1pv, 21 m; stn 296, 2pv, 26 m; stn 298, 1pv, 37 m; stn 299, 1pv, 35 m; stn 306, 1lv; stn 311, 3pv, 36 m; stn 312, 2pv, 26 m; stn 313, 2pv, 30 m; stn 316, 1pv, 68 m; stn 336, 1pv, 26 m; stn 340, 8pv, 1rv, 27 m; stn 341, 4pv, 3rv, 19 m; stn 344, 4pv, 37 m; stn 349, 1pv, 55 m; stn 357, 1pv, 77 m; stn 363, 1lv; stn 364, 1pv, 1rv, 49 m; stn 368, 1rv; stn 411, 1lv; stn 428, 1rv; stn 544, 1pv, 25 m; stn 545, 3pv, 37 m; stn 546, 2pv, 33 m; stn 547, 17pv, 1lv, 1rv, 29 m; stn 549, 2pv, 27 m; stn 550, 1pv, 26 m; stn 552, 1pv, 39 m; stn 554, 3pv, 25–29 m; stn 559, 1pv, 53 m; stn 572, 1pv, 67 m); Atoll de Huon (Lagon: stn 436, 1lv; stn 443, 1pv, 40 m); Atoll de Surprise (Lagon: stn 449, 1pv, 21 m; stn 455, 1pv, 40 m; stn 458, 1pv, 40 m; stn 465, 1pv, 1rv, 1lv, 45 m); Lagon Nord (Lagon: stn 478, 4pv, 35 m; stn 481, 5pv, 1rv, 1lv, 33 m; stn 482, 1pv, 33 m; stn 489, 1pv, 40–43 m; stn 504, 1lv; stn 520, 1pv, 37 m; stn 536, 1lv; stn 541, 1rv; stn 542, 2pv, 50 m; stn 542, 1lv); Ile de Pins (Lagon: stn 589, 2pv, 1lv, 1rv, 31 m; stn 591, 1pv, 16 m; stn 593, 1pv, 26 m; stn 594, 1pv, 27 m); Secteur de Yate (Lagon: stn 607, 1rv; stn 632, 1pv, 45 m; stn 634, 1pv, 36–42 m); Secteur de Thio (Lagon: stn 672, 1pv, 15–20 m; stn 687, 1pv, 40 m; stn 894, 1pv, 12 m); Secteur de Canala (Lagon: stn 696, 1pv, 57–41; stn 710, 1pv, 31 m; stn 715, 1pv, 35 m; stn 731, 2pv, 42 m; stn 749, 1rv, 1lv; stn 754, 1pv, 1rv, 36 m; stn 757, 1pv, 1rv, 44 m; stn 759, 1rv); Secteur de Poindimie (Lagon: stn 772, 1pv, 1lv, 30 m; stn 787, 1lv; stn 795, 1pv, 31 m; stn 800, 1pv, 33 m; stn 801, 1rv; stn 807, 1rv; stn 855, 2pv, 22 m; stn 855, 1pv, 22 m); Grand Recif Mengalia (Lagon: stn 851, 1lv; stn 859, 1lv; stn 865, 1pv, 24 m; stn 866, 1pv, 1rv, 26 m; stn 873, 1pv, 27 m; stn 864, 1pv, 1rv, 26 m; stn 870, 1pv, 37 m); Secteur de Pouebo (Lagon: stn 881, 1pv, 27 m; stn 885, 2pv, 32 m; stn 886, 1lv; stn 890, 2pv, 23 m; stn 891, 3pv, 1lv, 25 m; stn 898, 1pv, 22 m); Secteur de Koumac: (Lagon: stn 905, 1pv, 57 m; stn 910, 5pv, 26 m; stn 912, 2rv; stn 913, 2pv, 13 m; stn 915, 1lv; stn 916, 1pv, 13 m; stn 923, 1rv; stn 924, 1pv, 15 m; stn 936, 1pv, 15 m; stn 938, 1rv; stn 939, 6pv, 12 m; stn 940, 1pv, 1lv, 10 m; stn 942, 1pv, 15 m; stn 943, 2pv, 15 m; stn 946, 1pv, 17 m; stn 947, 2pv, 18 m; stn 951, 4pv, 1lv, 1rv, 12 m; stn 954, 1rv; stn 957, 1pv, 18 m); Secteur de Poum (Lagon: stn 961, 2pv, 20 m; stn 975, 2pv, 24 m; stn 976, 1pv, 1lv, 1rv, 20 m; stn 978, 1pv, 19 m; stn 980, 2lv, 1rv; stn 983, 1pv, 1lv, 68 m; stn 984, 8pv, 23 m; stn 985, 1pv, 17 m; stn 986, 1pv, 18 m: stn 990, 1pv, 23 m; stn 991, 1pv, 28 m; stn 995, 1pv, 36 m; stn

997, 1pv, 2rv, 1lv, 23 m; stn 1001, 1pv, 89 m; stn 1006, 2pv, 25 m; stn 1010, 1pv, 16 m; stn 1015, 1pv, 25 m; stn 1017, 2pv, 1lv, 21 m; stn 1002, 3pv, 78 m; stn 1007, 2pv, 24 m; stn 1025, 6pv, 28 m); Secteur de Balabio (Lagon: stn 1045, 1pv, 12 m); Secteur des Belep (Lagon: stn 1063, 3pv, 4rv, 2lv, 31 m; stn 1104, 1pv, 4lv, 1rv, 22 m; stn 1105, 3pv, 3rv, 6lv, 25 m; stn 1118, 1pv, 2rv, 3lv, 30 m; stn 1126, 2lv, 2rv, 41 m; stn 1134, 1pv, 40 m; stn 1139, 1pv, 39 m; stn 1140, 1lv; stn 1145, 13pv, 5rv, 4lv, 38 m; stn 1154, 3rv, 5lv, 40 m; stn 1156, 5rv, 3lv, 55 m; stn 1157, 1pv, 3lv, 2rv, 48 m; stn 1158, 1pv, 9rv, 2lv, 48 m; stn 1168, 3pv, 6lv, 4rv, 50 m; stn 1169, 1pv, 47 m; stn 1169, 2rv, 47 m; stn 1174, 1lv; stn 1181, 3pv, 3rv, 1lv, 45 m; stn 1182, 3pv, 1rv, 48 m; stn 1189, 1pv, 1lv, 20 m; stn 1190, 2rv, 2lv, 40 m; stn 1191, 1lv, 1rv; stn 1196, 4pv, 5lv, 4rv, 30 m; stn 1197, 1rv; stn 1198, 1pv, 42 m; stn 1205, 1pv, 38 m; stn 1217, 1pv, 2rv, 30 m). BANC CAPEL (Musorstom 5: stn DW264, 1rv). Ride des Loyaute: (Musorstom 6: stn DW430, 3pv, 2rv, 3lv, 30 m; stn DW431, 1pv, 21 m; stn DW434, 3pv, 1rv, 2lv, 23 m; stn DW435, 15pv, 3rv, 7lv, 32 m; stn DW436, 3pv, 1rv, 3lv, 33 m; stn 437, 3rv).

Remarks: Prashad (1932) outlined the taxonomic problems associated with this species. *Lioconcha ornata* has been confused in the literature by various authors. The typical *ornata,* as figured by recent authors (Abbott and Dance, 1982 [as *L. ornata* Lamarck, 1817]; Oliver, 1992; Lamprell and Whitehead, 1992), is attenuate posteriorly with an extended posterior margin and widely rounded ventral margin. However it should be noted that the species displays great inter-populational variation in shape, convexity and colour pattern. The name *Lioconcha picta* (Lamarck, 1818) has also been used by some authors for this species. Lamarck (1818) described *L. picta* from the same illustrations as Dillwyn's *ornata* (Lister Conchyliorum t.259. f.95 and Chemnitz Conchylien. 6. t.35. f.373, 376 and 381) and the latter name has priority. *L. ornata* (Lamarck, 1818) is a synonym of *L. castrensis* (Linnaeus, 1758).

Lioconcha (Sulcilioconcha) philippinarum (Hanley, 1844)

(Figure 2g–h)

Cytherea philippinarum Hanley, 1844: 110; Hanley, 1856: t.15, f.36.

Diagnosis: Shell solid, length to 27.7 mm. Sculpture of strong rounded, concentric ridges. Colour brown, with darker brown radial rays extending from the umbones; interior white.

Material examined: Nouvelle-Caledonie: Baie de St vincent (Lagon: stn 186, 1lv); Secteur de Canala (Lagon: stn 703, 1pv, 40 m); Grand Recif Mengalia (Lagon: stn 839, 2pv, 1lv, 37 m; stn 849, 1pv, 1lv, 1rv, 41 m); Secteur des Belep (Lagon: stn 1213, 1pv, 1rv, 32 m).

Remarks: The relatively few records of this species among this New Caledonian material appears to represent the southern limits of its range which extends through the Philippines to Japan.

Lioconcha (Sulcilioconcha) melharteae sp. nov.

(Figure 3a–c)

Etymology: Named for Dr Mel Harte in honour of her work on the Veneridae.

Diagnosis: Shell to 21 mm in length, 18.5 mm in height and 14.7 mm in width (paired valves); trigonally ovate, equivalve, inequilateral. Umbones situated anteriorly, moderately inflated and solid, oblique, prosogyrate. Lunule widely cordate, surrounded by an impressed line. Escutcheon long, narrow, impressed. Antero-dorsal margin short, steeply sloping, widely rounded terminally at the antero-ventral margin; postero-dorsal margin moderately convex, sharply sloping, broadly angulate posteriorly; ventral margin widely convex, slightly concave posteriorly. Shell with an ill-defined posterior fold extending from the umbones to the postero-ventral margin, with sculpture of dense

(approx. 80) flattened, concentric ribs which anastomose laterally and with irregular growth pauses; interstices between ribs very narrow, moderately deep. Periostracum white, thick and mostly confined to the margins. Hinge of left valve with anterior lateral tooth round and raised; anterior cardinal narrow, oblique and joined to median cardinal; median cardinal thick, moderately raised; posterior cardinal oblique, narrow; cardinal pit deep; inner margin ridged. Hinge of right valve with deep anterior lateral tooth pit; anterior cardinal narrow, raised, separated from the lower edge of the hinge plate, joined to median tooth at dorsal side of hinge plate; median cardinal narrow, peg-like; posterior cardinal bifid, oblique. Adductor muscle scars and pallial line poorly defined. External colour white, with blue-white growth pauses, usually with an orange ray extending from the umbones to the postero-ventral margin and an orange escutcheon and lunule. White specimens also occur often with tan-coloured zig-zag patterns. Internally the valves are glossy white with blue-white growth pauses showing through the shell surface.

Material examined: Holotype: MNHN – Nouvelle-Caledonie: Grand Recif Sud (Lagon: 1pv, stn 361, 22°36'S, 167°02'E, 29 Nov 1984, 78m). Length (anterior to posterior margin) 20.7mm, height (umbo to ventral margin) 18.3mm, width of conjoined valves 14.5mm.

Paratypes: MNHN – Nouvelle-Caledonie: Grand Recif Sud (Lagon: AM C305574, 3pv, stn 361, 22°36'S, 167°02'E, 29 Nov 1984, 78m; 1pv, 3lv, 1rv, stn 370, 22°38'S, 167°06'E, 30 Nov 1984, 127m; Lagon: 2pv, 2rv, stn 397, 22°39'S, 167°11'E, 23 Jan 1985, 125m; 1pv, 1lv, 1 rv, stn 429, 22°40'S, 167°15'E, 25 Jan 1985, 95m); Sud Nouvelle-Caledonie (Lagon SMIB: 6pv, 2rv, stn DW81, 22°38'S, 167°35'E, 9 Sept 1989, 110m); Lagon Nord (Lagon: 1pv, stn 484, 19°00'S, 163°35'E, 2 Mar 1985, 35m; 5pv, stn 517, 19°09'S, 163°35'E, 5 Mar 1985, 42m; 1pv, stn 522, 19°08'S, 168°38'E, 5 Mar 1985, 42m).

Other material examined: Plateau Chesterfield-Bellona (Chalcal 1: stn D14, 2rv, 1lv; stn 55, 1lv; stn 57, 1lv). Nouvelle-Caledonie: Grand Recif Sud (Lagon: stn 320, 2pv, 1rv, 1lv, 70 m; stn 367, 1lv; stn 368, 1lv; stn 369, 1lv; stn 370, 1pv, 3lv, 1rv, 127 m; stn 386, 1lv; stn 417, 1rv; stn 429, 1rv); Lagon Nord (Lagon: stn 484, 1pv, 35 m; stn 486, 1pv, 33 m; stn 531, 1pv, 1rv, 56 m); Secteur de Poindimie (Lagon: stn 772, 1pv, 1lv, 30 m); Secteur des Belep (Lagon: stn 1064, 1lv; stn 1099, 1lv; stn 1103, 3pv, 1lv, 1rv, 32 m; stn 1117, 7pv, 1lv, 36 m; stn 1129, 9pv, 1lv, 1rv, 40 m; stn 1168, 1lv; stn 1205, 1pv, 38 m).

Remarks: Compared with *Lioconcha philippinarum* (Hanley) and *L. dautzenbergi* (Prashad), *L. melharteae* sp. nov. has a far greater number of concentric, flattened ridges with narrow interstices (rounded, wider in *L. philippinarum* and separated by deep furrow-like interstices; much wider, rounder in *L. dautzenbergi* and with narrow, shallow interstices). In addition *L. melharteae* is always white externally while *L. philippinarum* and *L. dautzenbergi* are predominantly brown with some white zigzag patterns; internally these latter species are coloured whereas *L. melharteae* is glossy white.

Lioconcha (Sulcilioconcha) richerdeforgesi sp. nov.

(Figures 3d–f; 4a–b)

Etymology: Named for Bertrand Richer de Forges who led the ORSTOM expeditions.

Diagnosis: Shell to 11.25mm in length, 9.4mm in height and 6.7mm in width (paired valves); ovate, equivalve, slightly inequilateral. Umbones situated anteriorly; moderately inflated, fragile, prosogyrate. Lunule narrowly cordate, raised centrally, surrounded by an impressed line; escutcheon short, lanceolate, impressed. Antero-dorsal margin short, widely rounded to the antero-ventral margin; postero-dorsal margin moderately convex, slightly sloping, broadly rounded posteriorly; ventral margin widely rounded. Shell sculptured with dense, flattened concentric ribs which anastomose laterally; interstices narrow, shallow. Periostracum white, thick. Hinge of left valve with

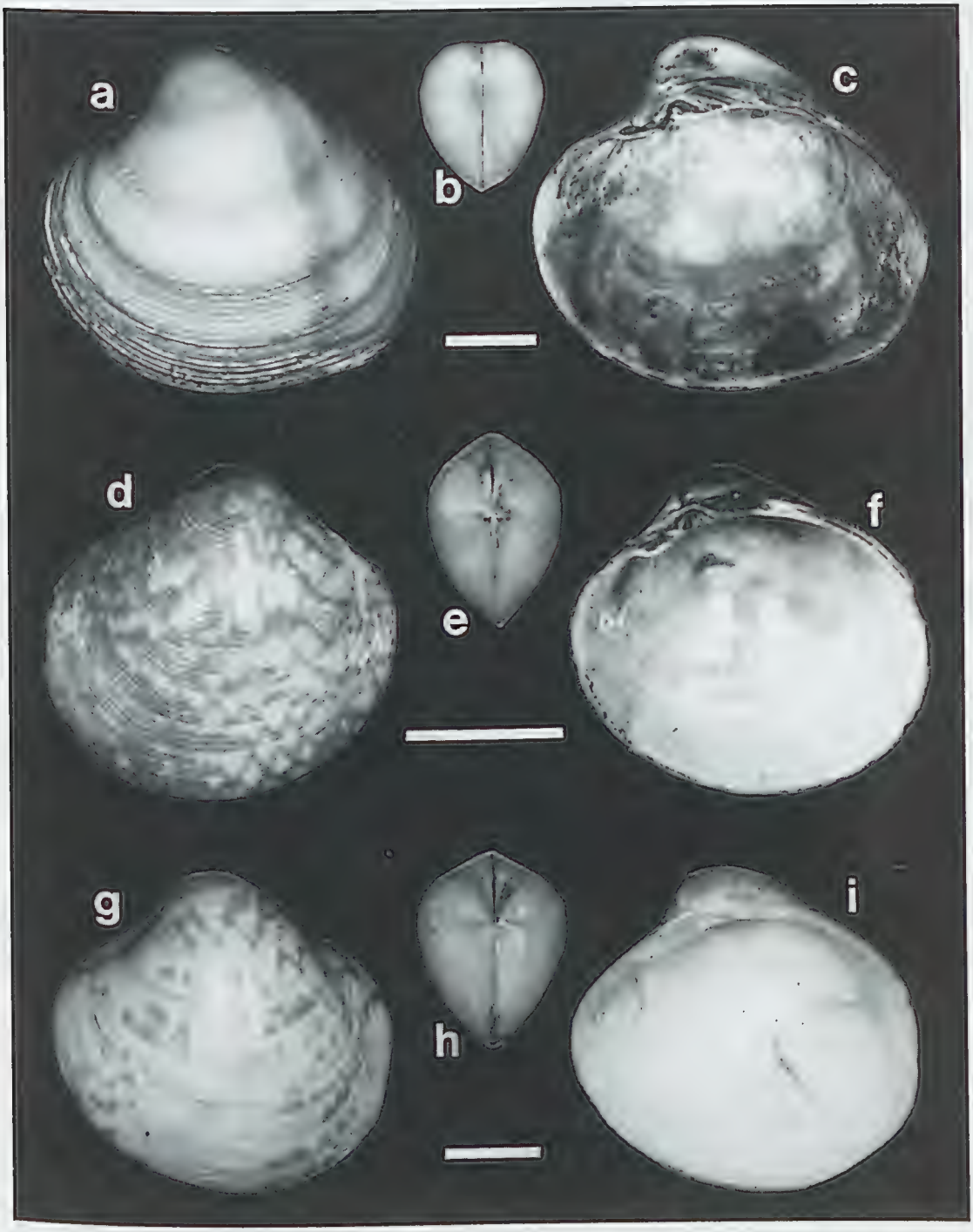

Figure 3. a–c. *Lioconcha (Sulcilioconcha) melhartae* sp.nov., holotype; d–f. *Lioconcha (S.) richerdeforgesi* sp.nov., Lagon: stn 876, paratype; g–i. *Pitar (Pitarina) healyi* sp.nov., holotype. Scale bars equal 5mm. Umbonal views not to scale.

anterior lateral tooth raised, peg-like; anterior cardinal oblique, thin, raised, joined to median cardinal towards the dorsal side of the hinge plate with a deep pit below their junction; median cardinal thick, raised, separated from the dorsal side of the hinge plate; posterior cardinal oblique, slightly curved, joined to dorsal side of hinge plate; inner margin ridged. Hinge of right valve with anterior lateral widely separated from the anterior cardinal (by lateral pit), anterior cardinal oblique, terminating at ventral edge of hinge plate, thin, raised, joined at dorsal side of hinge plate to median cardinal; median cardinal raised, slightly oblique, wider ventrally, separated from anterior and posterior cardinals by deep pits; posterior cardinal oblique, bifid, terminating short of ventral edge of hinge plate. Internal margins ridged, ridging stronger at the anterior and dorsal margins. Adductor muscle scars and pallial line poorly defined. Colouration: base colour white or tan with tan-brown or white v-shaped irregular markings over whole of shell surface; internally white with external colour patterns visible through the shell surface; escutcheon with tan-coloured chevron-shaped pattern crossing both valves.

Material examined: Holotype: MNHN – Nouvelle-Caledonie: Secteur de Pouebo (Lagon: 1pv, stn 876, 30–70m, 20°35'S, 164°51'E, 30–70 m, 13 Jan 1987). Length (anterior to posterior margin) 9.05 mm, height (umbo to ventral margin) 8.15 mm, width of conjoined valves 5.9mm.

Paratypes: MNHN – Nouvelle-Caledonie: Secteur de Poindimie (Lagon: 9lv, 8rv, many juveniles, stn 830, 105–110m, 20°49'S, 165°19'E, 10 Jan 1987); Secteur de Pouebo (Lagon: AM C305575, 2pv, 1rv, 1lv, stn 876, 30–70m, 20°35'S, 164°51'E, 13 Jan 1987).

Other material: Plateau Chesterfield-Bellona: (Chalcal 1: stn D21, 1lv). Nouvelle Caledonie: Grand Recif Sud (Lagon: stn 324, 1rv); Secteur des Belep (Lagon: stn 1104, 1rv).

Remarks: *Lioconcha richerdeforgesi* sp. nov. is more ovate than *L. philippinarum, L. dautzenbergi* and *L. melharteae,* and does not have the raised umbones of these species. *L. richerdeforgesi* is also more densely ribbed than *L. dautzenbergi* and *L. philippinarum* and lacks the strong brown colour of these species and the white colour with orange markings or with tan-coloured zigzag patterns of *L. melharteae.* The v-shaped, tan-coloured markings of *L. richerdeforgesi* readily separate it from the other species of *Lioconcha* (*Sulcilioconcha)* discussed here. Compared with *L. melharteae* (which it most closely resembles), *L. richerdeforgesi* has more numerous ribs, is less inflated, has the lunule noticeably narrower, the anterior margin more widely rounded and lacks an angulated posterior.

Pitar (Pitarina) citrina (Lamarck, 1818)

(Figure 4c–d)

Cytherea citrina Lamarck, 1818: 306.

Dione citrina Reeve, 1863: pl.10, fig.43.

Pitar (Pitarina) citrinus Lamprell and Whitehead, 1992: sp.520.

Dione ustulata Reeve, 1863: pl.11, fig.49.

Diagnosis: Shell solid, inflated, subtrigonal, length to 40 mm. Sculpture of fine concentric lirae. Colour orange, yellow or sometimes white, with purple posteriorly; interior white or purple, sometimes rayed posteriorly.

Material examined: Nouvelle-Caledonia: Nouméa (Pte aux longs cous, 3pv, J.Vidal; Platier Ouen Toro, 4lv, J.Vidal; Presqu'ile Nou, Anse Kuendu, 2pv, J.Vidal).

Remarks: *Pitar citrina* is widely distributed throughout the Indo-Pacific, it is a shallow-water species which was not represented in the expedition material but was donated to the MNHN from the J.Vidal collection.

Pitar (Pitarina) healyi sp. nov.
(Figure 3g–i)

Etymology: Named for Dr John Healy in honour of his contribution to Australian malacology.

Diagnosis: Shell to 17.15mm in length, 15.70mm in height and 10.85mm in width (paired valves); trigonally ovate, equivalve, almost equilateral, the umbones situated slightly anterior of the centre of the shell; inflated umbonally, moderately solid; umbones slightly oblique, curved forward; lunule large, cordate, raised centrally, striate, surrounded by an impressed line extending from under the umbones to the termination of the antero-dorsal margin; escutcheon not defined; antero-dorsal margin short, slightly convex, sharply sloping, rounded terminally; postero-dorsal margin slightly convex, sharply sloping, broadly angulate posteriorly; ventral margin widely convex; with an ill-defined postero-umbonal fold in each valve. Shell smooth, glossy with concentric microscopic striae and irregular growth lines; periostracum thin. Hinge of left valve with anterior lateral tooth strong, peg-like; anterior cardinal thin, acline, joined to median cardinal forming an inverted v-shaped socket; median cardinal solid, thick, oblique; posterior cardinal free, thin, oblique, parallel to ligament. Hinge of right valve with low anterior lateral tooth and deep socket to accommodate lateral tooth of left valve; anterior cardinal peg-like, narrow; median cardinal solid peg-like, wholly free; posterior cardinal oblique, long, slightly bifid. Adductor muscle scars and pallial line poorly defined, anterior adductor scar tear-shaped. Pallial sinus moderately shallow, wide, rounded terminally. External colour white, unpatterned or with interrupted orange-coloured zigzag patterns over the shell surface, umbones tinged with orange; periostracum chalky-white; interior white.

Material examined: Holotype: MNHN – Nouvelle-Caledonie: Secteur de Noumea (Lagon: 1pv, stn 29, 22°17'S, 166°34'E, 24m, 23 Mar 1984). Length 17.15mm, height 15.70mm, width (paired valves) 10.85mm.

Paratypes: MNHN – Plateau Chesterfield-Bellona (Chalcal 1: 1lv 2pv, stn D20, 19°11.60'S, 158°42.10'E, 67m). Nouvelle-Caledonie: Ile Ouen-Baie du Prony (Lagon: 1rv, stn 239, 22°24'S, 166°58'E, 43m, 23 Oct 1984); Grand Recif Sud (Lagon: AM C305576, 3pv, stn 315, 22°37'S, 166°53'E, 27 Nov 1984, 50m); Secteur de Yate (Lagon: 1rv, stn 619, 166°54'E, 22°03'S, 27–42m; 1pv, 2lv, stn 623, 22°01'S, 166°51'E, 6 Aug 1986, 32–40m; 1pv, stn 644, 21°52'S, 166°41'E, 48–45m); Secteur de Thio (Lagon: 3pv, stn 662, 21°44'S, 166°32'E, 8 Aug 1986, 50m; 3pv, 1lv, stn 664, 21°44'S, 166°29'E, 8 Aug 1986, 28–30m); Secteur de Poindimie (Lagon: 1lv, stn 808, 20°57'S, 165°30'E, 10 Jan 1987, 30m).

Other material examined: Plateau des Chesterfield: (Corail 2: stn DW63, 1rv, 1lv; stn DW107, 1rv; stn DW109, 1lv; stn DW115, 1lv; stn DW120, 1pv, 1rv, 325 m; stn DW157, 1lv); Plateau Chesterfield-Bellona (Chalcal 1: stn CP7, 1rv; stn D11, 1pv, 83 m; stn D22, 11pv, 68 m; stn D23, 1rv; stn D27, 2rv, 1lv, 67 m; stn D40, 1rv; stn D58, 1pv, 56 m; stn D60, 1pv, 45 m; stn 62, 1lv). Bancs Lansdowne-Fairway: (Corail 2: stn DW24, 1pv, 74–75 m; stn DW27, 1rv, 1lv; stn DW28, 1pv, 1lv, 78 m. Chalcal 1: stn D11, 1pv, 83 m; stn D62, 1lv). Nouvelle-Caledonie: Ile Ouen-Baie du Prony (Lagon: stn 69, 8pv, 13 m; stn 86, 1pv, 29 m; stn 92, 1pv, 24 m; stn 105, 1rv; stn 113, 6pv, 32 m; stn 120, 3rv, 1lv; stn 131, 1pv, 38 m; stn 146, 4pv, 40–52 m; stn 234, 7pv, 56 m); Secteur de Noumea (Lagon: stn 270, 1pv, 25 m); Grand Recif Sud (Lagon: stn 301, 6pv, 46 m; stn 314, 3pv, 46 m; stn 331, 1lv; stn 335, 3pv, 47 m; stn 349, 1pv, 55 m; stn 376, 2pv, 75–76 m; stn 403, 2pv, 45 m; stn 428, 1pv, 56 m; stn 567, 1pv, 51 m; stn 572, 2pv, 65 m); Lagon Nord (Lagon: stn 505, 1rv, 53 m; stn 509, 1pv, 49 m; stn 517, 1lv; stn 525, 1rv; stn 526, 1pv, 54 m; stn 528, 1lv; stn 529, 1pv, 50 m; stn 530, 2rv, 2lv; stn 533, 1pv, 1lv, 50 m; stn 534, 2pv, 1rv, 48 m; stn 542, 1pv, 50 m); Secteur de Yate (Lagon: stn 603, 1pv, 78–80 m; stn 614, 1pv, 48–50 m; stn 618, 1pv, 53–58 m; stn 640, 1lv; Secteur de Thio (Lagon: stn 652, 1lv; stn 662, 1pv, 50 m; stn 665, 1rv; stn 687, 1pv, 37–40 m; stn 692, 1pv, 33–38 m; stn 695, 1pv, 54–55 m); Secteur de Canala (Lagon: stn 723, 1rv; stn 727, 1pv, 45–46 m; stn 728, 1pv, 43–47 m); Secteur de Poindimie (Lagon: stn 801, 1pv, 29 m; stn 830, 42lv,

36 rv); Grand Recif Mengalia (Lagon: stn 847, 2pv, 28 m; stn 853, 1rv); Secteur de Pouebo; Lagon: stn 880, 3pv, 30–52 m); Secteur de Poum (Lagon: stn 995, 2pv, 36 m; stn 1022, 1pv, 25 m; stn 1023, 5pv, 27 m; stn 1025, 3pv, 28 m; stn 1028, 1rv); Secteur des Belep (Lagon: stn 1064, 4pv, 2lv, 29 m; stn 1065, 1pv, 3lv, 2rv, 28 m; stn 1067, 2pv, 28 m; stn 1070, 3pv, 1lv, 29 m; stn 1076, 3pv, 1lv, 31 m; stn 1077, 1rv; stn 1078, 1pv, 3rv, 4lv, 31 m; stn 1079, 2pv, 2lv, 1rv, 31 m; stn 1080, 5pv, 34 m; stn 1082, 1pv, 2lv, 3rv, 34 m; stn 1083, 1pv, 5lv, 8rv, 34 m; stn 1084, 5lv, 2rv; stn 1085, 11pv, 4lv, 3rv, 33 m; stn 1086, 7pv, 6rv, 1lv, 31 m; stn 1089, 12pv, 6rv, 6lv, 35 m; stn 1090, 11pv, 4lv, 4rv, 37 m; stn 1091, 11pv, 4rv, 3lv, 38 m; stn 1092, 4lv, 2rv, 37 m; stn 1093, 1lv; stn 1096, 9pv, 3lv, 1rv, 27 m; stn 1098, 4rv, 1lv; stn 1099, 6pv, 1rv, 38 m; stn 1101, 14pv, 39 m; stn 1102, 17pv, 6lv, 5rv, 38 m; stn 1103, 1pv, 32 m; stn 1107, 11pv, 41 m; stn 1108, 8pv, 1rv, 40 m; stn 1109, 5pv, 38 m; stn 1110, 3pv, 1lv, 31 m; stn 1112, 20pv, 42 m; stn 1113, 14pv, 1lv, 44 m; stn 1114, 24pv, 43 m; stn 1115, 1pv, 42 m; stn 1120, 6pv, 1rv, 47 m; stn 1121, 3pv, 1rv, 46 m; stn 1122, 14pv, 36 m; stn 1123, 8pv, 36 m; stn 1125, 13pv, 46 m; stn 1126, 1pv, 41 m; stn 1128, 3pv, 2rv, 26 m; stn 1130, 17pv, 53 m; stn 1131, 1pv, 53 m; stn 1132, 1lv; stn 1134, 5pv, 1rv, 40 m; stn 1137, 6pv, 51 m; stn 1136, 2pv, 50 m; stn 1138, 1pv, 42 m; stn 1141, 15pv, 1lv, 1rv, 53 m; stn 1142, 2pv, 54 m; stn 1143, 1lv, 1rv, 54 m; stn 1144, 8pv, 1lv, 2rv, 49 m; stn 1145, 1lv; stn 1157, 1pv, 48 m; stn 1160, 1pv, 65 m; stn 1162, 1pv, 1lv, 62 m; stn 1163, 6rv; stn 1164, 2rv; stn 1165, 1lv; stn 1166, 3pv, 63 m; stn 1167, 6pv, 5rv, 65 m; stn 1168; 2pv, 2rv, 50 m; stn 1170, 1rv, 1lv; stn 1171, 6lv, 3rv; stn 1172, 2lv; stn 1173, 2pv, 2lv, 2rv, 64 m; stn 1174, 6pv, 1lv, 53 m; stn 1175, 2pv, 1lv, 1rv, 62 m; stn 1176, 1lv; stn 1179, 1pv, 62 m; stn 1181, 1pv, 45 m; stn 1183, 6pv, 58 m; stn 1184, 1pv, 60 m; stn 1187, 6pv, 51 m; stn 1188, 22pv, 1rv, 33 m; stn 1189, 1pv, 20 m; stn 1190, 5pv, 1lv, 40 m; stn 1191, 13pv, 45 m; stn 1192, 5pv, 45 m; stn 1193, 3pv, 52 m; stn 1194, 4pv, 57 m; stn 1196, 1pv, 30 m; stn 1199, 3pv, 43 m; stn 1206, 1pv, 36 m; stn 1200, 3pv, 41 m; stn 1201, 18pv, 33 m; stn 1205, 2pv, 38 m; stn 1211, 2pv, 35 m; stn 1214, 1pv, 29 m); Sud Nouvelle-Caledonie (Lagon: stn 48, 6pv, 9rv, 8lv, 28 m).

Remarks: *Pitar healyi* sp. nov. is consistent in shape but variable in colour, ranging from pure, glossy white to being strongly patterned with orange or orange-brown zigzag patterns. It is most similar to *P. nancyae* Lamprell and Whitehead (1990) and *P. sophiae* (Angas, 1877) with which it occurs sympatrically. *P. healyi* differs from those species in being much more inflated, higher in proportion to length and less elongate. *P. healyi* is also similar in shape to *P. nipponica* Kuroda and Habe, 1971 and *P. japonicus* Kuroda and Kawamoto, 1956 but is smaller, more angulate posteriorly and has an umbonal-postero fold which is absent in those species.

Pitar (Pitarina) pellucidus (Lamarck, 1818)

(Figure 4e–f)

Cytherea pellucidus Lamarck, 1818: 313.

Dione australica Reeve, 1863: pl.11, fig.47.

Pitar (Pitarina) pellucidus (Lamarck); Lamprell and Whitehead, 1992: sp.516.

Diagnosis: Shell thin, length to 45 mm; similar to *P. affinis*, but much thinner and more inflated; the umbones are often tinged light brown with a purple spot beneath them.

Material examined: Plateau des Chesterfield: (Corail 2: stn DW100, 1rv; stn DW112, 1pv, 58 m; stn DW164, 1lv). Nouvelle-Caledonie: Ile Ouen-Baie du Prony (Lagon: stn 63, 2pv, 20 m. Lagon: stn 243, 1pv, 29 m); Secteur de Noumea (Lagon: stn 275, 1pv, 19 m; stn 281, 3pv, 10 m); Grand Recif Sud (Lagon: stn 562, 1rv); Atoll de Surprise (Lagon: stn 457, 1pv, 38 m); Secteur de Yate (Lagon: stn 625, 1pv, 34–40 m; stn 641, 1rv); Secteur de Poindimie (Lagon: stn 781, 1lv; Grand Recif Mengalia stn 853, 1pv, 27 m; stn 873, 1lv).

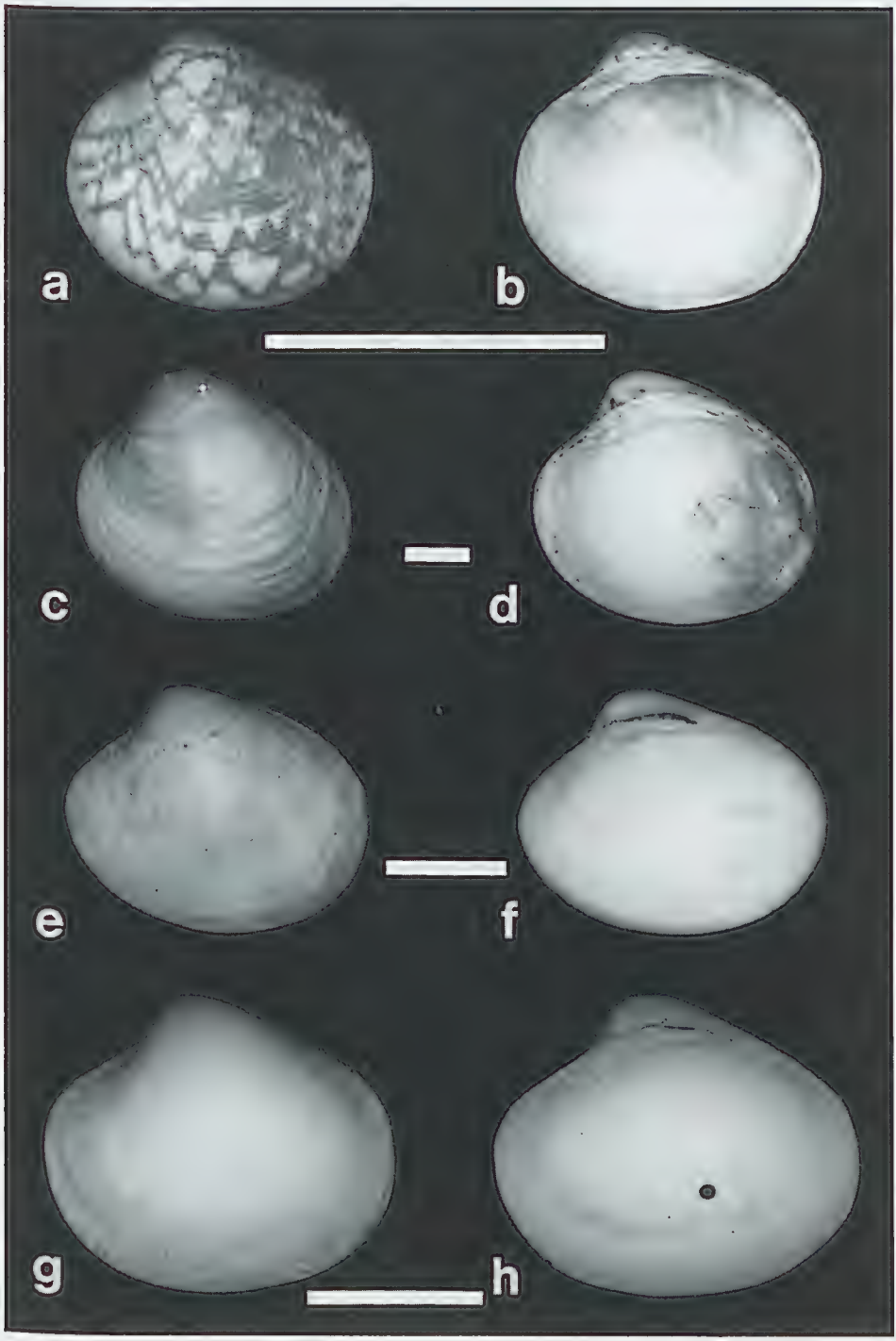

Figure 4. a–b. *Lioconcha (Sulcilioconcha) richerdeforgesi* sp. nov., holotype; c–d. *Pitar (Pitarina) citrina* (Lamarck), Noumea, J. Vidal; e–f. *Pitar (P.) pellucidus* (Lamarck), Lagon: stn 853; g–h. *Pitar (P.) noguchii* Habe, Lagon: stn 495. Scale bars equal 10mm.

Remarks: *Pitar pellucidus* is very variable in shape and colour, ranging from pure white to cream, usually with tan-coloured zigzag patterning, while the umbones are usually tinged with brown with a purple spot ventral to them. This is a widespread Indo-West Pacific, shallow-water species which has a relatively poor representation in the expedition material.

Pitar (Pitarina) noguchii Habe, 1958
(Figure 4g–h)

Pitar (Agriopoma) noguchii Habe, 1958: 34.

Pitar (Pitarina) noguchii Habe; Habe, 1964: pl.58, fig.6.

Diagnosis: Shell thin, inflated, length to 20 mm. Sculpture of fine concentric ridges and irregular growth pauses, with small puncture marks over surface. Colour white internally and externally. Similar to *nipponica* but differs in having a truncate posterior margin and in being more inflated.

Material examined: Plateau des Chesterfield: (Corail 2: stn DW112, 1pv, 225 m). Bancs Lansdowne-Fairway: (Corail 2: stn DW21, 2pv, 1lv, 77 m; stn DW28, 1lv). Nouvelle-Caledonie: Grand Recif Sud (Lagon: stn 375, 1pv, 67–71 m); Atoll de Huon (Lagon: stn 439, 3lv, 2rv); Secteur de Thio (Lagon: stn 667, 1pv, 33–37 m); Secteur de Canala (Lagon: stn 698, 1pv, 43 m; stn 711, 1pv, 56 m; stn 749, 1pv, 49 m; stn 760, 1pv, 43 m); Secteur de Poindimie (Lagon: stn 763, 1pv, 42 m; stn 771, 1pv, 34 m; stn 773, 1pv, 1rv, 1lv, 48 m; stn 779, 1rv, 1lv; stn 780, 1pv, 33 m; stn 786, 1rv, 1lv; stn 795, 1pv, 31 m; stn 814, 1lv; stn 820, 1rv; stn 824, 1pv, 1lv, 30 m; stn 833, 2pv; stn 836, 1pv); Grand Recif Mengalia (Lagon: stn 840, 2rv, 2lv; stn 855, 1pv, 22 m; stn 856, 1pv, 30 m); Secteur de Pouebo (Lagon: stn 882, 1pv, 30–40 m); Secteur des Belep (Lagon: stn 1156, 1lv).

Remarks: Hitherto only recorded from Japan; these records are a significant range extension for the species.

Pitar (Pitarina) affinis (Gmelin, 1791)
(Figure 5a–b)

Venus affinis Gmelin, 1791: 3278.

Cytherea inflata Sowerby, 1853: 637, fig.89; pl.133, figs 127–128.

Pitar (Pitarina) affinis (Gmelin); Lamprell and Whitehead, 1992: sp.514.

Diagnosis: Shell solid, length to 50 mm. Sculpture of very fine growth pauses, glossy. Colour white or cream with tan-brown blotches and rays centrally and towards the umbones, purple spots sometimes beneath umbones; sometimes markings are absent; interior cream.

Material examined: Plateau des Chesterfield: (Corail 2: stn DW121, 1pv, 1lv, 34 m). Nouvelle-Caledonie: Baie de St vincent (Lagon: stn 166, 1pv, 10 m); Atoll de Surprise (Lagon: stn 469, 1pv, 39 m); Secteur de Pouebo (Lagon: stn 900, 1pv, 40 m); Secteur de Koumac (Lagon: stn 921, 1rv); Secteur de Poum (Lagon: stn 972, 1lv, 1rv); Secteur des Belep (Lagon: stn 1069, 1lv; stn 1105, 1pv 1lv, 25 m; stn 1196, 1rv; stn 1213, 1rv). Ride des Loyaute: (Musorstom 6: stn DW433, 1rv; stn DW436, 1rv).

Remarks: *Pitar affinis* is a common species in the Philippines and northern Australia. These records are an eastward extension of its range.

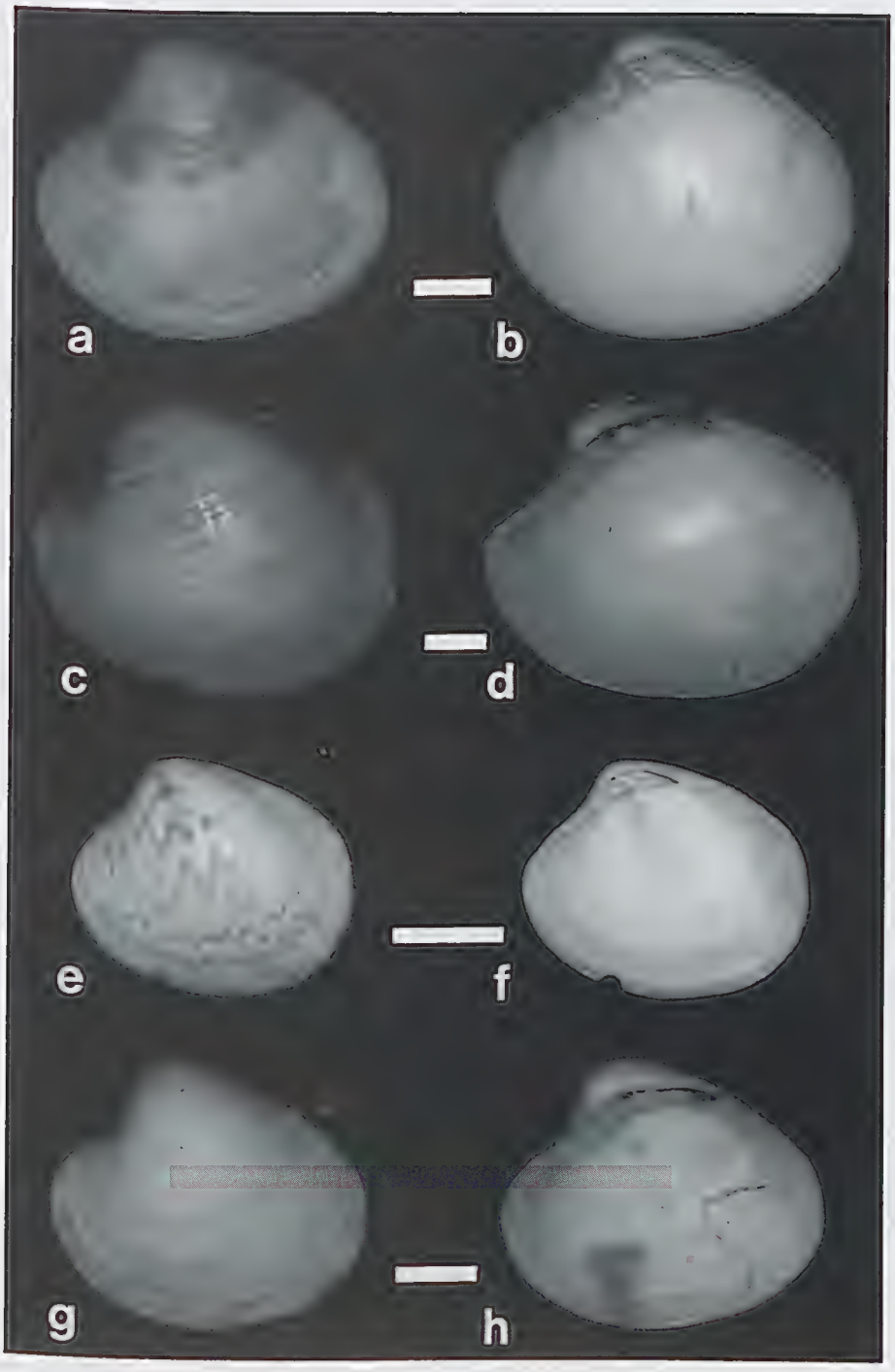

Figure 5. a–b. *Pitar (Pitarina) affinis* (Gmelin), Lagon: stn 469; c–d. *Pitar (P.) prora* (Conrad), Noumea, J. Vidal; e–f. *Pitar (P.) spoori* Lamprell and Whitehead, Corail 2: stn DW94; g–h. *Pitar (P.) japonicum* Kuroda and Kawamoto, Corail 2: stn DW21. Scale bars equal 10 mm.

Pitar (Pitarina) prora (Conrad, 1837)
(Figure 5c–d)

Venus prora Conrad, 1837: 253, pl.19, fig.18.

Pitar (Pitarina) prora (Conrad); Lamprell and Whitehead, 1992: sp.513.

Diagnosis: Shell solid, length to 65 mm, lunule large. Sculpture of even, fine, concentric striae and growth lines. Colour white or cream, internally and externally; some smaller specimens have fine tan radial chevron patterns.

Material examined: Nouvelle-Caledonie: Secteur de Poindimie (Lagon: stn 762, 1pv, 1lv, 43 m; stn 834, 1pv, 58 m); Presqu'ile Nou, Anse Kuendu, 22°14'S, 166°22'E, J.Vidal, October, 1989.

Remarks: *Pitar prora* is the species with the largest and heaviest shell in the subgenus *Pitarina*. *P. prora* appears to be an uncommon species throughout its range.

Pitar (Pitarina) spoori Lamprell and Whitehead, 1990
(Figure 5e–f)

Pitar (Pitarina) spoori Lamprell and Whitehead, 1990: 42, fig.3a–d; Lamprell and Whitehead, 1992: sp.519.

Diagnosis: Shell length to 35 mm; similar to *pellucidus* and *subpellucidus*, but more quadrate and with a different colour pattern. Colour of anterior white, with sparse interrupted brown radial rays; a wide brown radial ray covers the posterior; the escutcheon is marked by a few, spaced brown lines; a deep brown spot often occurs beneath the umbones.

Material examined: Plateau des Chesterfield: (Corail 2: stn DW94, 2pv, 36–53 m). Nouvelle-Caledonie: Secteur de Yate (Lagon: stn 643, 1pv, 56–66 m); Secteur de Poindimie (Lagon: stn 835, 1pv, 1rv, 135–150 m); Secteur des Belep (Lagon: stn 1118, 1lv).

Remarks: These records include the first live-collected specimens of *Pitar spoori*. Previously, this species was only known from dead shells taken in the littoral zone of north Queensland (Lamprell and Whitehead 1990).

Pitar (Pitarina) japonicum Kuroda and Kawamoto, 1956
(Figure 5g–h)

Pitar (Agriopoma) japonicum Kuroda and Kawamoto, 1956: 89, figs1–4.

Pitar (Pitarina) japonicus (Kuroda and Kawamoto); Lamprell and Whitehead, 1992: sp.522.

Diagnosis: Shell thin, subtrigonal, length to 35 mm. Sculpture of fine concentric growth lines. Colour cream-white, with pale orange or pink umbones and interior.

Material examined: Plateau des Chesterfield: (Corail 2: stn DW60, 1rv). Bancs Lansdowne-Fairway: (Corail 2: stn DW20, 1lv; stn DW21, 2pv, 1lv, 86 m). Nouvelle-Caledonie: Lagon Nord (Lagon: stn 496, 1rv, 1lv).

Remarks: These New Caledonian records of *Pitar japonicus* mark the southern limit of its distribution which extends from Japan to northern Australia.

Pitar (Pitarina) nancyae Lamprell and Whitehead, 1990
(Figure 6a–b)

Pitar (Pitarina) nancyae Lamprell and Whitehead, 1990: 45; fig.3e–h: Lamprell and Whitehead, 1992: sp.526.

Diagnosis: Shell thin, length to 30 mm; similar to *affinis* but with a thinner shell, more elongate profile and darker colour markings. Colour white, with wide, broken rays of brown; lunule and escutcheon sparsely marked with brown zigzag pattern; umbones purple tipped; interior white, with a small, livid purple spot inside the umbones.

Material examined: Plateau Chesterfield-Bellona: (Chalcal 1: stn D56, 1pv, 60 m). Bancs Lansdowne-Fairway (Chalcal 1: stn CP1, 1lv). Nouvelle-Caledonie: Grand Recif Sud (Lagon: stn 548, 1pv, 33 m); Lagon Nord (Lagon: stn 542, 1rv); Secteur de Thio (Lagon: stn 668, 2pv, 1rv, 40 m); Secteur de Canala (Lagon: stn 702, 2pv, 37 m); Secteur de Poindimie (Lagon: stn 787, 1pv, 39 m; stn 836, 1pv, 57 m); Secteur de Pouebo (Lagon: stn 902, 1pv, 32 m).

Remarks: Previously recorded from the coasts of central to north Queensland, these records of *Pitar nancyae* represent a significant range extension. The species usually occurs in depths ranging from 20–30 m, however the specimens collected from this expedition ranged from 33–60 m.

Pitar (Pitarina) sophiae (Angas, 1877)
(Figure 6c–d)

Cytherea sophiae Angas, 1877: 176, pl.26, f.23.

Pitar (Pitarina) sophiae (Angas); Lamprell and Whitehead, 1992: sp.531.

Diagnosis: Shell thin, inflated, length to 17 mm. Sculpture of concentric growth lines, smooth, glossy. Colour white, with grey concentric bands, sometimes with faint brown broken rays; umbones usually tinged with red anteriorly, visible internally.

Material examined: Bancs Lansdowne-Fairway: (Corail 2: stn DW19, 1rv). Nouvelle-Caledonie: Secteur de Noumea (Lagon: stn 13, 1pv, 20 m); Ile Ouen-Baie du Prony (Lagon: stn 133, 1pv, 59–62 m; stn 146, 1pv, 40–52 m; stn 234, 5pv, 1lv, 56 m; stn 238, 1lv); Grand Recif Sud (Lagon: stn 429, 2rv); Secteur de Yate (Lagon: stn 606, 2pv, 1lv, 48 m; stn 608, 1rv; stn 621, 1rv); Secteur de Thio (Lagon: stn 650, 1lv; stn 676, 1pv, 41 m; stn 692, 2pv, 48 m); Secteur de Canala (Lagon: stn 696, 1rv; stn 716, 1rv; stn 726, 1pv, 51 m; stn 729, 1pv, 1lv, 45 m; stn 759, 1rv); Secteur de Poindimie (Lagon: stn 771, 1pv, 34 m; stn 780, 1rv; stn 801, 1pv, 29 m; stn 821, 2lv; stn 830, 2lv, 8rv; stn 835, 1rv); Grand Recif Mengalia (Lagon: stn 847, 2pv, 28 m; stn 865, 1rv).

Remarks: Smith (1885) considered *Pitar sophiae* to be a synonym of *Cytherea hebraea* Lamarck, 1818. However comparison of specimens of *P. sophiae* in the Australian Museum and the type of *P. hebraea* in the Museum National d'Histoire Naturelle, Geneve shows that *P. sophiae* is longer in proportion to height than *P. hebraea*, is more widely rounded at the anterior and posterior margins, does not attain the size of *P. hebraea*, has a pink flush on the inner side of the valves of many specimens and has a different colour pattern. Additionally, the pallial sinus in *P. hebraea* is wider, deeper and less ascending than in *P. sophiae*.

Pitar (Pitarina) potteri Healy and Lamprell, 1992
(Figure 6e–f)

Pitar (Pitarina) potteri Healy and Lamprell, 1992: 79; fig.1e–h; Lamprell and Whitehead, 1992: sp.515 (as *Pitar* sp.)

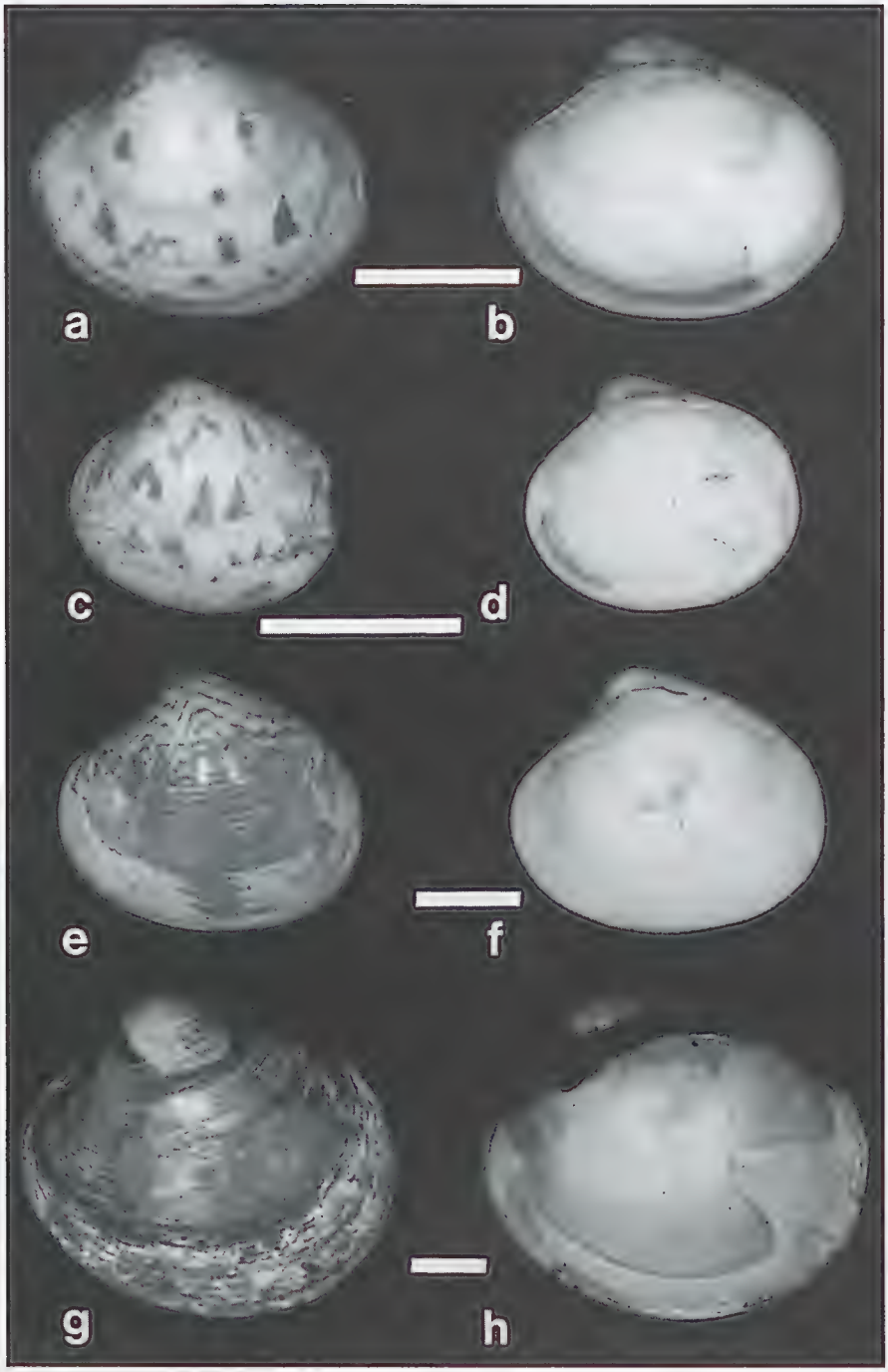

Figure 6. a–b. *Pitar (Pitarina) nancyae* Lamprell and Whitehead, Lagon: stn 702; c–d. *Pitar (P.) sophiae* (Angas), Lagon: stn 13; e–f. *Pitar (P.) potteri* Healy and Lamprell, Musorstom 6: stn DW432; g–h. *Pitar (Hyphantosoma) intricata* (Dautzenberg), Lagon: stn 28. Scale bars equal 10 mm.

Diagnosis: Shell solid, inflated, length to 38 mm; similar to *affinis*, but smaller and more inflated. Sculpture of microscopic concentric growth striae. Colour cream-white with faint tan zigzag patterns near umbones; interior white.

Material examined: Ride des Loyaute: (Musorstom 6: stn DW432, 1pv, 21 m; stn DW437, 1rv).

Remarks: *Pitar potteri* is another species hitherto known only from north Queensland waters.

Pitar (Hyphantosoma) intricata (Dautzenberg, 1907)
(Figure 6g–h)

Meretrix (Pitar) intricata Dautzenberg, 1907: 333, pl.v, fig.1.

Diagnosis: Shell solid, inflated, length to 53 mm; similar to *spoori*, but larger, more inflated with stronger concentric sculpture and less quadrate than that species. Sculpture of dense concentric ridges crossed by zigzag grooves, weaker medially. Colour light-brown to white externally, internally white.

Material examined: Nouvelle-Caledonie: Secteur de Noumea (Lagon: stn 28, 1pv, 9 m).

Remarks: *Pitar intricata* has hitherto only been recorded from the Celebes and Japan.

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Three new morphologically and genetically determined species of hydrobiid gastropods from Dalhousie Springs, northern South Australia, with the description of a new genus

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A new genus (*Dalhousia*) containing two new species (*D. globosa* and *D. harrisi*), and a new species of *Fluvidona* (*F. centralia*) are described from Dalhousie Springs in northern South Australia. Allozyme data from 77 populations are presented and used to justify the separation of the two species. *Dalhousia* is the sister group of *Fonscochlea* from the Lake Eyre Supergroup springs but differs from that genus in females having a single sperm pouch. Species of *Fluvidona* are otherwise found in streams and rivers, mainly in south eastern Australia, *F. centralia* being the only species known from central Australia. The anatomy of the three species is described and a summary of their variation, based on shell measurements and allozymes, is presented.

Introduction

There are many artesian springs associated with the Great Artesian Basin (GAB) in South Australia (Ponder, 1986; Boyd, 1990) and they are of great interest, biologically, limnologically and geologically. Their considerable conservation significance has been recognised (Harris, 1981, 1993; Ponder, 1985, 1986, 1995; DEST, 1994).

Two major groups of artesian springs are associated with the section of the GAB in South Australia. The largest group, the Lake Eyre Supergroup (Habermehl, 1982; Ponder, 1986), lies in a line running roughly south west between Marree and Oodnadatta. The other major group, Dalhousie Springs, comprises approximately 80 springs in a small area (about 70 km^2) of far northern South Australia which together have the largest natural discharge of water from the GAB (Habermehl, 1982; Smith, 1989). Aspects of their history, biology, limnology and geology are described in Zeidler & Ponder (1989). The springs contain a number of endemic aquatic animals, including fishes (Glover, 1989; Crowley & Ivantsoff, 1990), amphipods (Zeidler, 1989, 1991) and hydrobiid gastropods (Ponder, 1989 and herein). The latter are by far the most abundant and conspicuous of the endemic aquatic invertebrates, as is the case in other GAB artesian springs (see below) and also in some spring systems in the Americas (e.g. Hershler, 1985; Hershler and Landye, 1988; Hershler and Sada, 1987). These snails are generally associated with long-term permanent water (Ponder, 1994).

A study on the hydrobiid snails of the Lake Eyre Supergroup springs demonstrated considerable morphological and genetic diversity (Ponder *et al.*, 1989; in press) and hydrobiids from springs associated with the Queensland part of the GAB have been described by Ponder and Clark (1990).

A major survey of Dalhousie Springs was undertaken in 1985, the results presented in Zeidler and Ponder (1989). In a review of the aquatic molluscs of Dalhousie, Ponder (1989) recognised an undescribed fauna of "at least six species of hydrobiid snails" based on gross shell differences, but noted the extremely variable shell morphology encountered in the springs. Major differences in shell size and shape were noted between populations inhabiting different environments, even associated with a single spring. Preliminary morphological analysis indicated that standard techniques were not able to distinguish putative taxa. A second major survey of the fauna was undertaken in 1990 to

collect material for electrophoretic examination. In all, 77 samples were subsequently analysed. These results, combined with an analysis of shell measurement data for most of these samples, are presented here. Aspects of the genetic results obtained from the Dalhousie samples, particularly relating to gene flow, have been published elsewhere (Colgan and Ponder, 1994).

In this paper three taxa are described, two congeners (the common snails found in the springs) are separated using allozyme differences, and a third is a member of a separate genus (*Fluvidona*) and is restricted to a few small seepages and cold outflows.

Material and methods

Collection. Material was collected by hand from many springs and each collection site for the

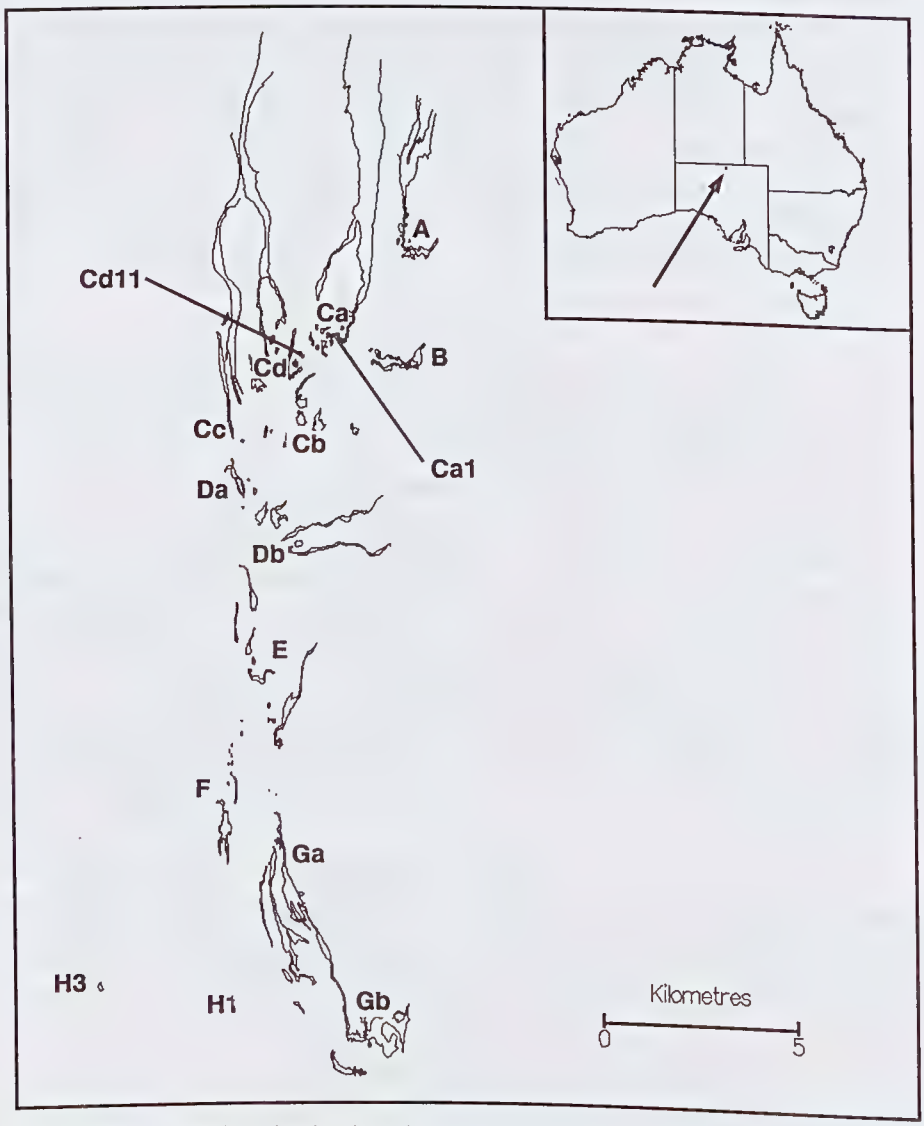

Figure 1. Map of Dalhousie Springs showing the springs from which samples were obtained for this study.

material used in the genetic analysis is listed in Appendix 1 (see also Ponder, 1989 for overall locality details). Latitudes and longitudes have been calculated using a GIS system (MapInfo ver. 5.01; Mapping Information Systems, 1985–1991), after digitizing the spring details based on the locality map in Zeidler and Ponder (1989, fig. 2). The spring numbers used follow Zeidler and Ponder (1989) and are shown in Fig. 1.

Morphology studies. Dissection and preparation of material for SEM were by standard methods (Ponder *et al.*, 1993). Morphological observations presented here for the three new species are based on the type populations. The majority of populations have also been examined in less detail to confirm the main anatomical characters and a summary of their shell measurements and ratios are presented (Appendix 2).

Shell measurements were obtained using the methods described by Ponder *et al.* (1989), those parameters measured being listed below. The number of opercular pegs was counted only in the species of *Fluvidona*, those in the new genus being too ill-formed in many specimens to count accurately. In the statistics given in each description male and female shell measurements have been pooled and the range of morphology taken from the total pool of data available for that locality. These are given separately in the measurement tables presented for each type lot and in Appendix 2 (Tables 2 and 3). Statistical analysis was performed using SYSTAT (Wilkinson, 1992). Material is held in the South Australian Museum, Adelaide (SAM) and the Australian Museum, Sydney (AMS).

Abbreviations used in tables of measurements:

AL – shell aperture length; AW – shell aperture width; BW – length of last (body) whorl of shell; CV – convexity ratio of penultimate whorl of shell; OL – length of operculum; OS – length of white opercular smear; OW – width of operculum; PH – height of longest opercular peg; PL – length of area occupied by opercular pegs; PN – number of opercular pegs; SL – shell length; SW – shell width; TW – number of teleoconch whorls.

Electrophoresis. Standard methods for cellulose acetate electrophoresis were used (Richardson *et al.*, 1986; Hebert and Beaton, 1989; Ponder *et al.*, 1991). Snails were homogenized in about 20 µl (10 µl for small individuals) of buffer, providing enough sample for up to 12 gels. Where more than one locus encoding the same enzyme was found, they were designated numerically in order of decreasing mobility. Allozymes identified for each locus within a species are designated in the same way. The enzymes scored for each species, together with abbreviations, Enzyme Commission Numbers, and the number of loci are listed in Table 1. The computer package BIOSYS-1 (Swofford and Selander, 1989) was used to assist analysis.

Table 1. The numbers of interpretable loci. The columns give the enzyme name, its abbreviation, E.C. number and the number of interpretable loci for: A, *Dalhousia* spp.; and B, *Fluvidona*.

ENZYME	ABBREVIATION	E.C. NO.	A	B
Alcohol dehydrogenase	ADH	1.1.1.1	1	
Alkaline phosphatase	ALKP	3.1.3.1	1	1
Aspartate aminotransferase	AAT	2.6.1.1	2	2
Enolase	ENO	4.2.1.11	1	1
Esterase	EST	3.1.1.1	3	3
Fumarate hydratase	FH	4.2.1.2	1	
ß-Galactosidase	GAL	3.2.1.23	1	
Glycerol-3-phosphate dehyd.	GPD	1.1.1.8	1	1
Glucosephosphate isomerase	GPI	5.3.1.9	1	1
Glutamate-pyruvate transamin.	GPT	2.6.1.2	1	
Hexokinase	HK	2.7.1.1	1	
Hydroxybutyrate dehydrogenase	HBDH	1.1.1.30	1	
Isocitrate dehydrogenase	IDH	1.1.1.42	2	2
Leucine aminopeptidase	LAP	3.4.11	1	
Malate dehydrogenase	MDH	1.1.1.37	2	2

Mannosephosphate isomerase	MPI	5.3.1.8	1	1
Peptidases: Phe-Pro substrate	PPR	3.4.11	1	1
: Leu-Ala substrate	LAL	3.4.11	1	
: Leu-Leu-Gly substrate	LGG	3.4.11	2	
Phosphoglucomutase	PGM	5.4.2.2	2	2
6-Phosphogluconate dehydrog.	6-PGDH	1.1.1.44	1	1
Sorbitol dehydrogenase	SDH	1.1.1.14	2	2
Triosephosphate isomerase	TPI	5.3.1.1	1	1
UDP glucose pyrophosphorylase	UDPG	2.7.7.9	1	1

Results

Taxonomy

Three new species in two genera, one new, are described below, as are the electrophoretic results confirming the status of these species.

Dalhousia n. gen.

Type species: *Dalhousia globosa* n. sp.

Diagnosis: Hydrobiids with simple, smooth, imperforate, broadly ovate to conic shell, with simple aperture and lacking external varix. Operculum with weakly to moderately-developed pegs on inner side and radula with two laterally placed basal cusps on central teeth. Female genital system with single globular, posteriorly-located medium-sized sperm sac and posteriorly elongated coiled oviduct. Male with long, tapering (whip-like) penis. Stomach with horn-like process on upper edge of posterior chamber and lacking obvious caecum.

Description: Shell (Figs 2A–C, F–H, 3–5) simple, smooth, imperforate, broadly ovate to conic, with simple oval aperture and lacking external varix. Protoconch (Fig. 6A,B) of about 1.5 whorls, sculptured with irregular, shallow pits. Operculum (Fig. 7A–E) thin, flat, with white smear and weakly to moderately-developed pegs on inner side. Body heavily pigmented (mainly black), cephalic tentacles with narrow, median-dorsal unpigmented line (corresponding to line of dorsal cilia) and narrow unpigmented zone at base of tentacles. Mid-dorsal strip of cilia rather weakly-developed and set in a narrow, shallow groove (Fig. 8B,C); three more strongly developed cilial strips ventrally, two ventro-lateral and one mid-ventral (Fig. 8A,B). Snout (Fig. 9A–D) with little or no cilia dorsally, some cilial tufts latero-ventrally. Labial area weakly papillate, papillae with very short cilia-like processes (Fig. 9D).

Anatomy generally similar to *Fonscochlea* (Ponder *et al.*, 1989). Columellar muscle short and wide. Ctenidium large, with numerous broadly triangular filaments, posterior end usually slightly overlapping anterior edge of pericardium. Osphradium oval, short, behind middle of ctenidium. Hypobranchial gland very narrow, weakly to moderately developed. Rectum straight or slightly arched in pallial cavity, with longitudinally orientated faecal pellets and, usually, partially overlapping pallial oviduct glands. Radula (Fig. 10) with 2 pairs of basal cusps on central teeth, otherwise typical of family. Stomach (Fig. 11) with characteristic "horn"-like process on upper edge of posterior chamber with caecum rudimentary or absent. Renal organ protruding partly into pallial roof, renal opening usually with white lips, renal gland longer than wide. Prostate gland (Fig. 12A,B) broadly oval, much higher (*i.e.* dorso-ventral dimension) than thick, mostly visceral, with pallial vas deferens opening near posterior pallial wall. Penis (Figs 12C, 13) long, tapering, whip-like, with pointed distal end. Penial duct (Fig. 12C) undulating in small, moderately expanded basal section, straight in long distal part. Female reproductive system similar to *Fonscochlea* but with only a single globular sperm sac (Fig. 14, sps). Coiled oviduct (Fig. 14A,B, co) with simple, U-shaped proximal part, long posterior extension, wrapped around sperm sac in S-shaped coil; proximal part

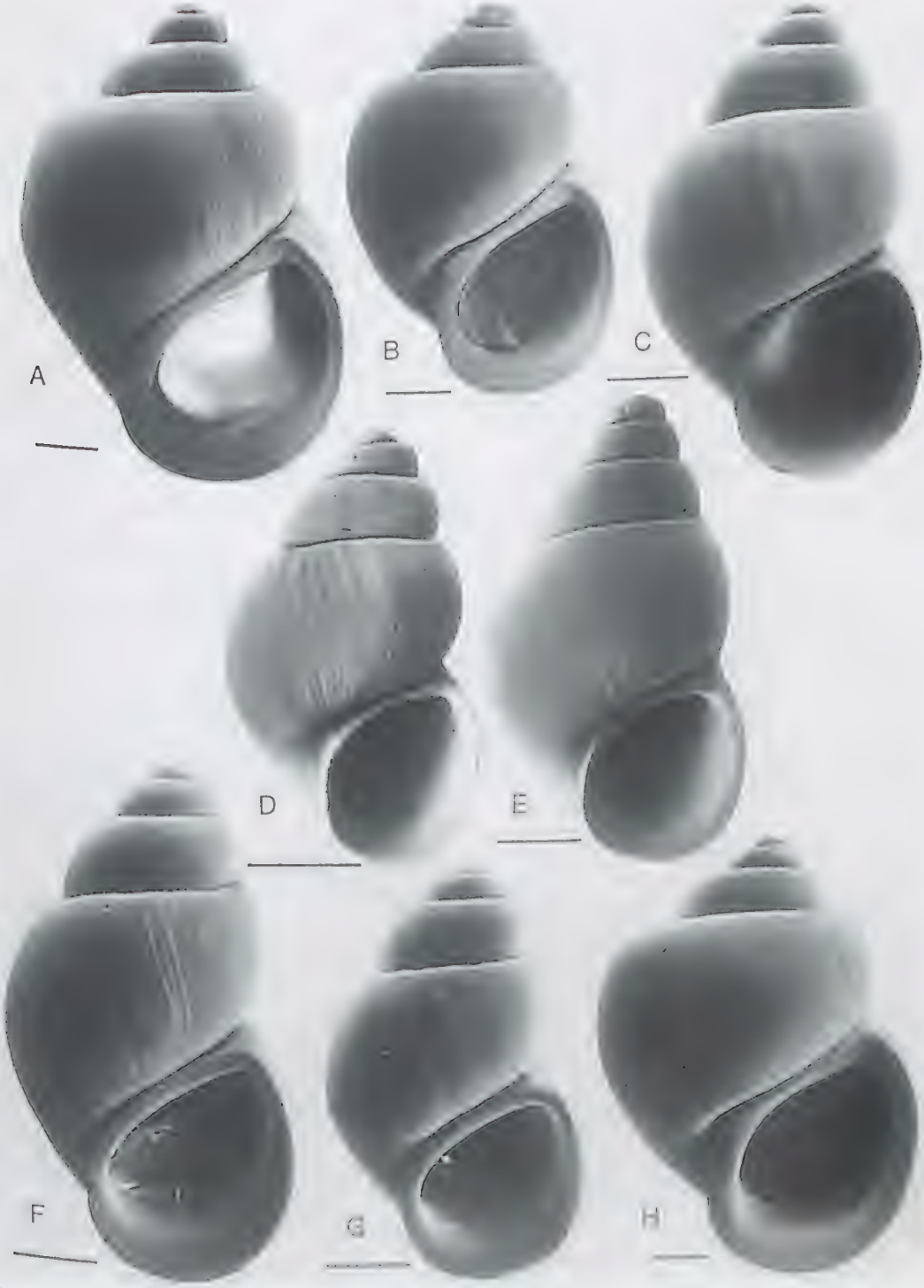

Figure 2. Shells of *Dalhousia* species and *Fluvidona centralia*. A–C,F,G. *D. harrisi*. A, holotype; B, paratype; C, Spring Ca13A; F,G, Spring Ca7 (station C643). D,E. *F. centralia*. D, holotype; E, lower outflow of Spring E1 (station D62). H, *D. globosa*, holotype. Scales 0.5mm.

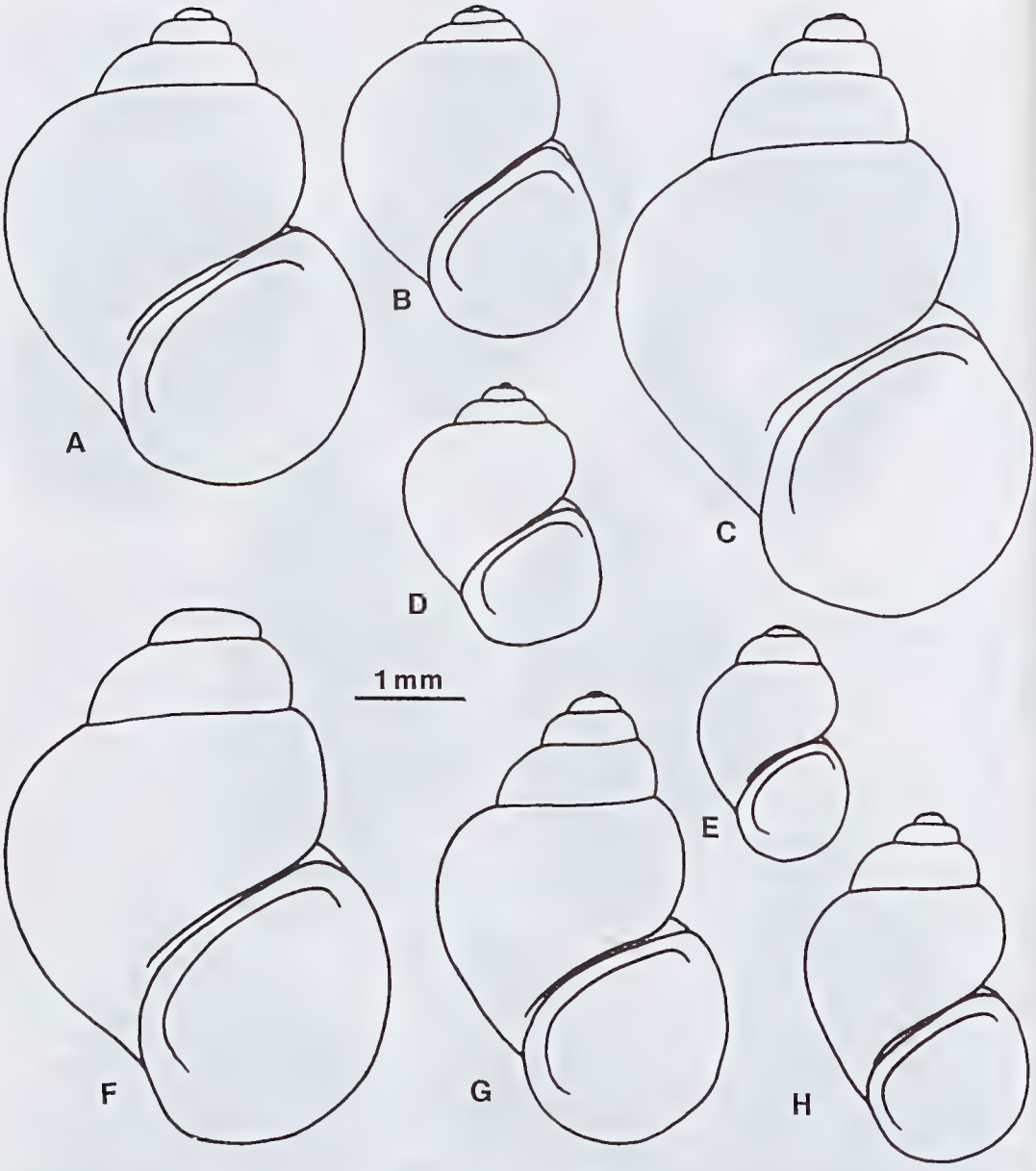

Figure 3. Shells of *Dalhousia globosa*. A. Spring Ca1 (station D26), B. Spring Ca1 (station D46), C, D. Spring Cd1 (station D43), E, H. Spring Ca1a (station D24), F. Spring A1 (station D4A), G. Spring Cb2 (station D51).

of this duct containing stored sperm (Fig. 14C,D, sp); duct to sperm sac very short. Common duct (Fig. 14, cd) very long. Pallial oviduct simple, with or without distinct glandular zones, opening small, terminal (Fig. 14A,B, po). Nervous system typical of family, with long supra-oesophageal connective and suboesophageal ganglion abutting left pleural ganglion.

Remarks. The anatomy of the new genus is generally similar to that described in detail for other Australian hydrobiids (*Fonscochlea* Ponder *et al.*, 1989; *Tatea* Ponder *et al.*, 1991; and *Fluvidona*

Ponder *et al.*, 1994). However, *Dalhousia* differs from these genera, and other hydrobiid genera, in the combination of characters listed in the diagnosis. Most similar to *Fonscochlea*, the new genus can be readily distinguished by its apomorphic single sperm sac and very elongate penis. When superimposed on the cladogram produced by Ponder and Clark (1990) *Dalhousia* is the sister taxon to *Fonscochlea*.

Dalhousia globosa n. sp.

Figs 2H, 3, 6A,B, 7A,B, 8C, 9A, 10B–D,F, 11B, 12A,C, 13A, 14A,C, 16A,C,D, 22, 23, 24.

Ponder, 1989, figs 11.1F, 11.2B,C,G.

Etymology. Globosa – globus, globulus, Latin – ball, sphere.

Type locality. Ca1, the main spring (Earwanyera Spring), Dalhousie Springs, South Australia.

Collection details of type material. Stn. C641B–C, Spring Ca1, 26°24'29"S 135°31'08"E, on rocks & wood from shallow water. 28/5/1983, Coll. W. Ponder & W. Zeidler.

Holotype, SAM, D18937, paratypes, SAM, 18938, AMS, C.201743(C641B), C.201750(C641C).

Diagnosis: Typically with large, globose shell. Distinguished electrophoretically from the next species in having very high frequencies of the LAP 2, PGM–2 3, SDH–1 1 and SDH–2 2 allozymes, and a high frequency of the GPI 2 allozyme.

Description: Shell (Fig. 2H, 3). Shell opaque, small (1.7–4.6 mm in length, mean in type series 4.1), broadly conical to globose, SW/SL 0.67–0.97 (overall mean 0.79, 0.77 in type series), AL/SL 0.46–0.69 (mean 0.55), sutures impressed, whorls usually narrowly shouldered. Protoconch (Fig. 6A,B) of about 1.5–1.6 whorls, minutely punctate. Teleoconch of 2.8–4.2 (mean 3.3) strongly convex whorls, sutures impressed; sculpture of indistinct growth lines only. Aperture slightly longer than wide, AW/AL 0.78–1.06 (mean 0.92, 0.94 in type series), angled posteriorly. Peristome with sharp edge, moderately thickened internally, entire, with inner lip attached to parietal wall. Colour (imparted by periostracum) pale yellow to yellow-brown. There is no significant sexual dimorphism in shell size in the type population.

Dimensions of holotype.

	SL	SW	AL	AW	BW	TW
Holotype	4.16	3.35	2.36	2.06	3.45	3.2

Dimensions of specimens from paratype series

Female, N=13

	SL	SW	AL	AW	BW	CV	TW
Minimum	3.61	2.97	2.08	1.93	3.10	0.18	3.0
Maximum	4.52	3.52	2.42	2.23	3.61	0.26	4.2
Mean	4.11	3.20	2.21	2.08	3.43	0.23	3.3
S.D.	0.25	0.18	0.11	0.10	0.16	0.02	0.34

Male, N=7

	SL	SW	AL	AW	BW	CV	TW
Minimum	3.57	2.86	1.96	1.90	3.09	0.20	2.75
Maximum	4.61	3.30	2.43	2.17	3.73	0.25	3.50
Mean	4.09	3.09	2.19	2.04	3.42	0.23	3.21
S.D.	0.38	0.17	0.19	0.09	0.23	0.02	0.25

Summarised shell dimensions of an additional 200 specimens from various points within Spring

Ca1 are given in Appendix 2. Note that the mean size is considerably smaller than those of the pool population (Fig. 16C).

Operculum (Fig. 7A,B). Ovate, thin, pale yellow, with eccentric nucleus, usually with 4–5 small, weak pegs on white smear on inner side.

Statistics of 20 opercula from the type series.

Female, N=13

	OL	OW	OS	PL	PH
Minimum	1.55	1.13	0.44	0.10	0.05
Maximum	1.79	1.36	0.86	0.48	0.15
Mean	1.69	1.28	0.65	0.34	0.09
S.D.	0.07	0.07	0.13	0.09	0.03

Male N=7

	OL	OW	OS	PL	PH
Minimum	1.56	1.17	0.42	0.23	0.06
Maximum	1.80	1.35	0.73	0.49	0.13
Mean	1.68	1.25	0.58	0.36	0.09
S.D.	0.11	0.08	0.10	0.09	0.03

Radula (Fig. 10B–D,F). Central teeth broad, each with 3–4 (usually 4) small, triangular cusps on either side of a sharp median cusp about twice the length of the adjacent cusps. Two pairs of lateral basal denticles present, innermost larger. Lateral teeth with largest cusps in tooth row, 3–4 on inner side of large triangular median cusp and 3–4 (usually 3) on outer side. Inner marginal teeth with 20+ narrow, sharp cusps on antero-distal and outer-distal edge. Outer marginal teeth with small, narrow, sharp cusps (approx. half length of those on inner marginal teeth) on antero-distal and inner-distal edge.

Head-foot. Cephalic tentacles pigmented dorsally, with narrow unpigmented mid-dorsal stripe; snout and dorsal neck also pigmented. Ciliation (Figs 8C, 9A) as for generic description. Foot, and especially opercular lobes, weakly pigmented; pallial roof and visceral coil variable but usually black or mottled with grey or black.

Anatomy. Osphradium unpigmented, located at posterior quarter of ctenidium, narrowly oval, 0.27-0.42 mm in length. Ctenidium with 30-37 broadly triangular filaments, apices central to towards right; maximum width 0.46–0.76 mm, posterior 2–3 filaments overlapping pericaridum. Rectum straight in pallial cavity in both sexes. Renal organ extending 1/3 (rarely 1/4) length of renal gland into pallial roof; renal gland 0.65–0.92 mm in length, 0.32–0.43 mm in width. Pericardium extending 1/4 to 1/3 of length into pallial roof. Stomach (Fig. 11B) with style sac 0.76–0.92 mm in length, stomach proper 0.77–0.89 mm in length, caecum absent or rudimentary.

Testis of 1.8–2.0 whorls; seminal vesicle visible externally and lies between digestive gland and testis for only 0.2–0.3 whorls behind stomach, convolute over stomach. Prostate gland (Fig. 12A) 0.54–0.62 mm in length (about 0.06–0.15 mm in pallial roof), 0.35–0.48 mm in height, broadly oval, narrowly oval in section. Pallial vas deferens coiled, forming densely pigmented (grey to black – darker than surrounding epithelium of neck) low, rope-like ridge across neck at base of penis; with few undulations nearer prostate, straight immediately anterior to, and beneath, prostate. Penis (Figs 12C, 13A) unpigmented or with proximal part of distal section of penis with grey pigmentation, basal section unpigmented or with some grey pigment; distal section long and evenly tapering, basal section relatively small, expanded. Penis base 0.37–0.49 mm from right eye, just to right of midline of head.

Ovary of 1.1–1.2 whorls. Coiled oviduct (Fig. 14A,C, co) with 1 distal U-shaped loop, orientated anteriorly; distal part straight, posteriorly wrapped around sperm sac (Fig. 14A, sps) in S-shape coil. Duct to sperm sac ventral, very short (virtually direct communication). Common duct (Fig. 14A,C,

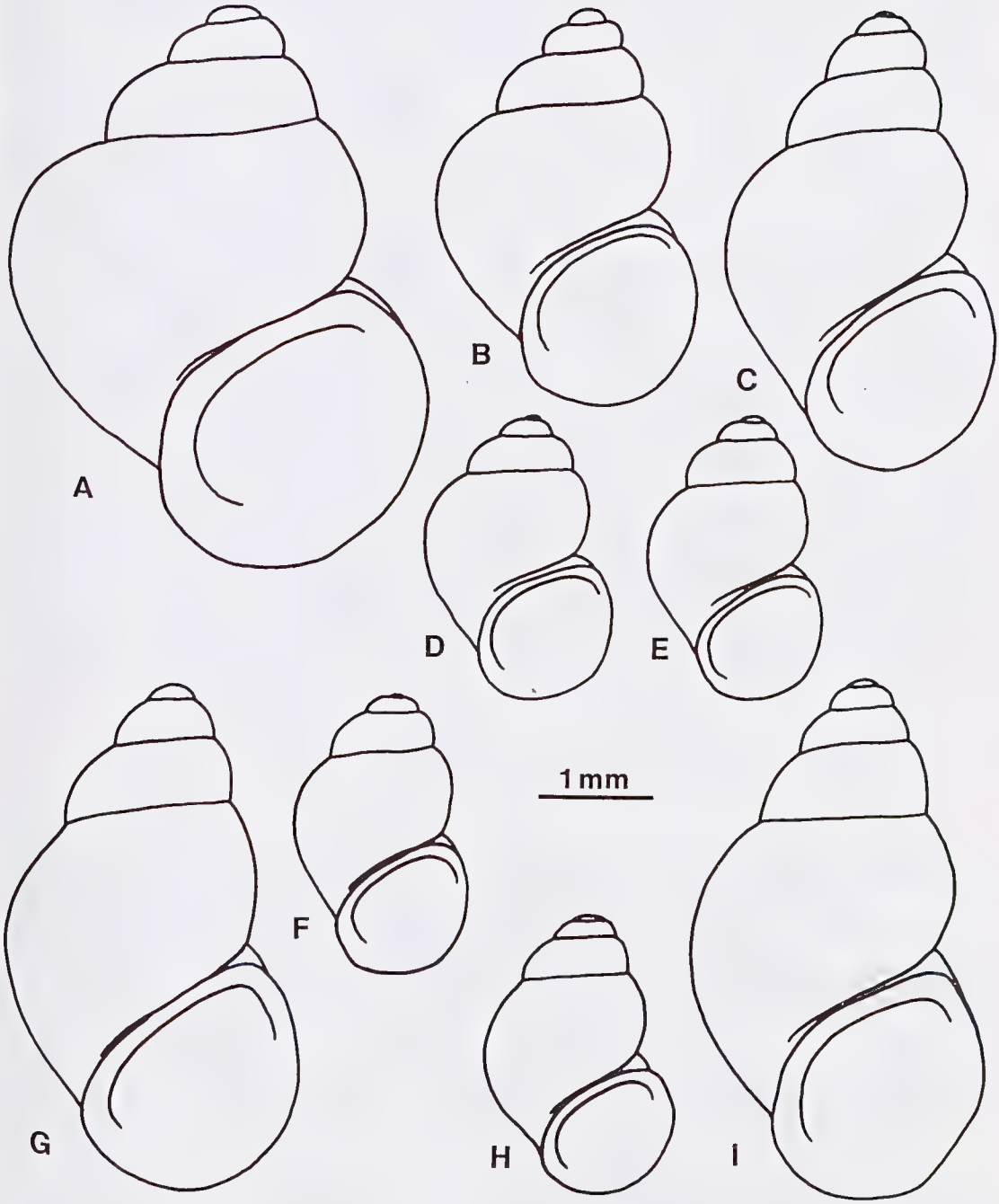

Figure 4. Shells of *Dalhousia harrisi*. A, B, D. Spring Ca5 (station D75), C, E. Spring Db2 (station D20), F, G. Spring Ga6B (station D16), H, I. Spring F1 (station D54).

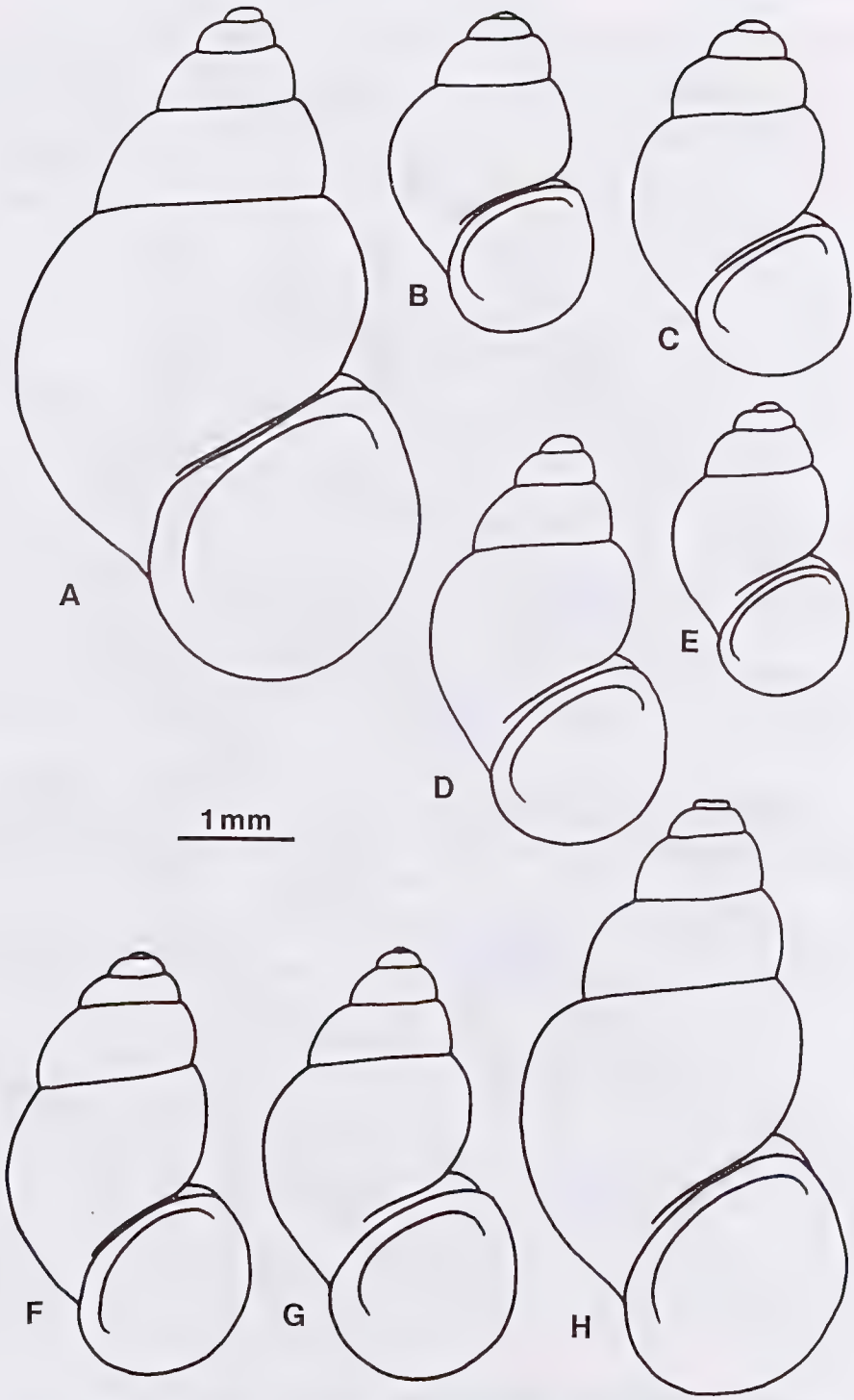

Figure 5. Shells of *Dalhousia harrisi*. A, B. Spring Ca3 (station D76), C. Spring A1 (station D4A), D. Spring E2 (station D7), E, G, H. Spring B2 (station D74), F. Spring H3 (station D19).

cd) very long, straight. Sperm sac globular, 0.34–0.46 mm in maximum length, 0.17–0.39 mm in maximum width. Albumen gland (Fig. 14A) 0.96–1.23 mm in length, 1/10–1/7 of length in pallial roof; slightly shorter than capsule gland. Capsule gland rounded anteriorly, oval in section, 1.16–1.39 mm in length, with indistinct glandular zones. Ventral channel narrow, lacking distinct vestibule, small, short opening slightly behind anterior end of capsule gland.

Distribution (Fig. 15). Common in main pool and outflow of Spring Ca1. Springs confirmed as containing this species are listed in Table 7 (Appendix 3) and include only members of the A, B, Ca, Cb, Cc, and Cd groups.

This species mostly lives in large warm pools or warm outflows from large springs ranging from 33–42°C (the majority 35–40°C).

Remarks. Data from allozyme electrophoresis presented below show, when using the criterion of sympatry, that there is no justification for recognising more than two species-group taxa within *Dalhousia*. Both are very variable in shell morphology, although *D. globosa* is generally larger and wider than the species described below. There are no known anatomical characters that can be consistently used to separate these two taxa. The allozyme differences summarized in the diagnosis are detailed below. Because of the difficulty in species-level determination and somewhat hazy species boundaries, we have selected specimens for the type series of the two species of *Dalhousia* named here from one of a few populations in which they are known to be sympatric.

There is a considerable range of variation in shell size and shape (Fig. 3. 16A,C; and Ponder, 1989, figs 11.1F, 11.2B,C,G) within this species, even within the same spring (Fig. 3A,B, 16C) or the same sample (Fig 3C,D). Mean shell length, in the seven measured populations, ranges from 2.5 to 4.27 mm (Appendix 2, Table 2) with considerable variance in some samples (Appendix 2, Table 2; Fig. 16A,C), and many populations differ significantly ($P<0.001$) from conspecific populations in length and other dimensions and ratios. Overall there is a difference between sexes in most shell dimensions and ratios ($P<0.1$). Allozyme variation within this taxon is detailed below (see also Appendix 3, Table 7).

Dalhousia harrisi n. sp.

Figs 2A–C, F,G, 4, 5, 7C–E, 8A,B, 9B–D, 10A,E, 11A, 12B, 13B–D, 14B,D, 15, 16B,D, 17, 22–24.

Ponder, 1989, figs 11.1A–E,G, 11.2A,D,E.

Etymology. Named for Colin Harris, as a small recognition of his efforts in the conservation of the mound springs of South Australia.

Type locality. Ca1, the main spring (Earwanyera Spring), Dalhousie Springs, South Australia.

Collection details of type material. Stn Ca1 We, Spring Ca1, 26°24'29"S 135°31'08"E, fringe of roots on steep edge at water surface on side of main pool. 12/6/1985, Coll. W. Ponder & D. Winn.

Holotype, SAM, 18939, paratypes, SAM 18940, AMS, C201744.

Diagnosis. Typically with small to medium, conical to ovate-conic shell. Distinguished electrophoretically from *D. globosa* in having high frequencies of LAP 3, SDH-1 2, SDH-2 1 and PGM-1 4 allozymes.

Description. Shell (Figs 2A–C,F,G, 4, 5). Shell opaque, small (length 2.3–3.8 mm, mean 2.8 mm, 3.1 in type series), ovate-conic to conic, SW/SL 0.64–0.80 (mean 0.71), AL/SL 0.47–0.57 (mean 0.51). Suture impressed, whorls convex to very slightly shouldered. Protoconch of about 1.5–1.6 whorls, minutely punctate. Teleoconch of 2.6–3.6 (mean 3.1) convex whorls, sutures impressed; sculpture of indistinct growth lines only. Aperture slightly longer than wide, AW/AL 0.87–1.01 (mean 0.94, 0.91 in type series) and angled posteriorly. Peristome entire,with sharp edge, weakly thickened internally, with inner lip attached to, or slightly separated from, parietal wall. Colour

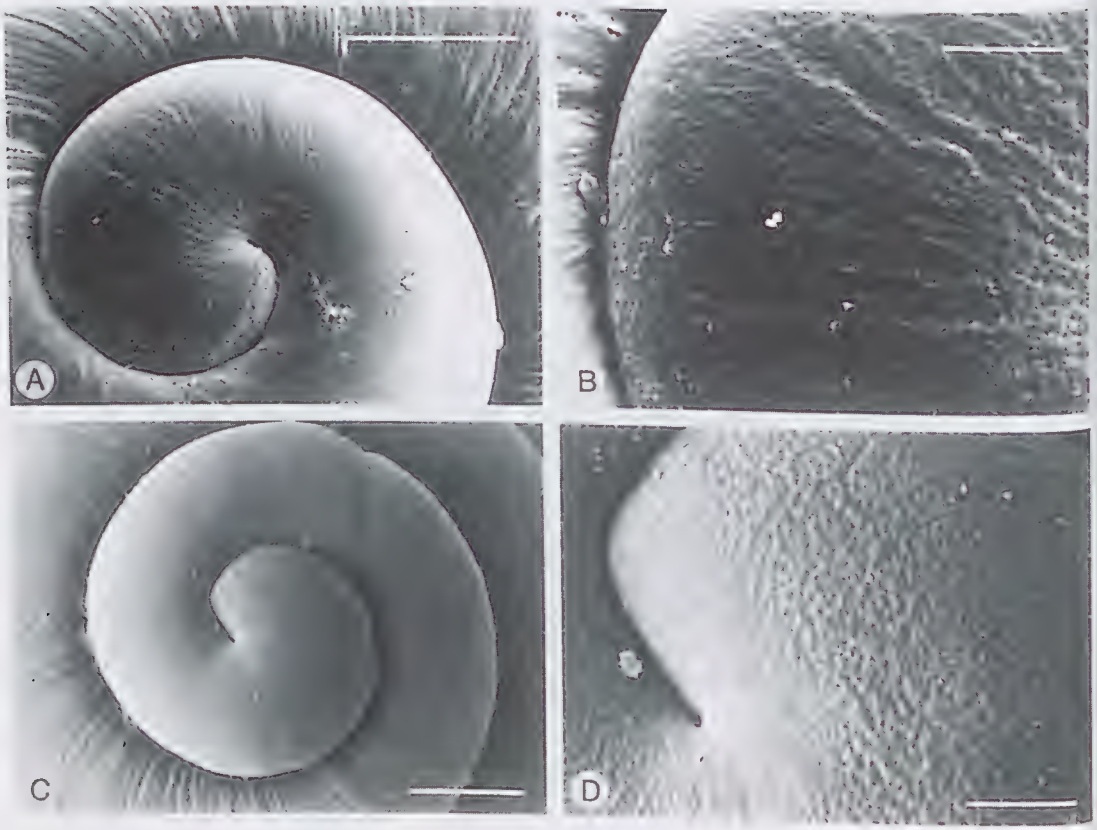

Figure 6. Protoconchs of *Dalhousia* species and *Fluvidona centralia*. A,B. *Dalhousia globosa*, Spring Ca1. C,D. *F. centralia*, Spring E1 (station D62). Scales A,C – 0.1mm, B,D – 0.025mm.

(imparted by periostracum) yellow-brown (some populations very dark brown or orange brown depending on environment). There is no significant sexual dimorphism in shell size in the type population.

Dimensions of holotype.

	SL	SW	AL	AW	BW	TW
Holotype	3.20	2.52	1.79	1.52	2.69	2.6
Figured paratype (AMS, C.201745)	3.92	2.90	2.09	1.95	3.23	3.0
Figured specimens						
(Ca13A) (AMS, C.201746)	2.92	1.74	1.39	1.10	2.33	3.5
(Ca7) (AMS, C.201747)	2.60	1.72	1.26	1.10	2.15	3.1
	3.22	2.00	1.53	1.30	2.50	3.5

Figure 7. Opercula of *Dalhousia* species and *Fluvidona centralia*; all from inner side. A,B. *D. globosa*, Spring Ca1 (station 641c). C–E. *D. harrisi*. C, topotype (station Ca1We), D, Spring Ca13A, E, Spring Ca7 (station C644). F–H. *F. centralia*. F,G, paratypes, H, Spring E1, lower outflow (station D62). Scales 0.2mm.

Dimensions of specimens from paratype series

Females, N=11

	SL	SW	AL	AW	BW	CV	TW
Minimum	2.68	1.86	1.35	1.29	2.19	0.12	2.6
Maximum	3.70	2.60	1.88	1.64	3.01	0.19	3.6
Mean	3.16	2.28	1.64	1.49	2.60	0.16	3.1
S.D.	0.27	0.19	0.13	0.10	0.21	0.02	0.27

Males, N=9

	SL	SW	AL	AW	BW	CV	TW
Minimum	2.57	1.89	1.32	1.25	2.14	0.14	2.8
Maximum	3.45	2.53	1.79	1.59	2.77	0.19	3.6
Mean	3.00	2.16	1.55	1.41	2.45	0.16	3.2
S.D.	0.30	0.22	0.17	0.11	0.22	0.02	0.20

Shell dimensions of 50 topotypes are given in Appendix 2, along with those of additional populations of this species.

Operculum (Fig. 7C–E). Ovate, pale yellow, thin, with eccentric nucleus, with 0–5 small, weak pegs on white smear on inner side.

Statistics of 20 opercula from the type series.

Females, N=11

	OL	OW	OS	PL	PH
Minimum	1.11	0.70	0.30	0.12	0.05
Maximum	1.53	1.12	0.53	0.32	0.13
Mean	1.32	0.92	0.39	0.22	0.09
S.D.	0.12	0.11	0.07	0.06	0.03

Males, N=9

	OL	OW	OS	PL	PH
Minimum	1.11	0.77	0.26	0.17	0.07
Maximum	1.38	1.05	0.55	0.27	0.14
Mean	1.24	0.88	0.36	0.22	0.10
S.D.	0.09	0.10	0.09	0.03	0.03

Radula (Fig. 10A,E). As for *D. globosa* but central teeth usually with 3 (range 3–4) cusps on either side of the median cusp.

Head-foot. Cephalic tentacles pigmented dorsally, with or without narrow unpigmented mid-dorsal stripe; snout and dorsal neck also pigmented. Ciliation (Fig. 8A,B, 9B–D, 13C) as for generic description. Foot and opercular lobes pigmented; pallial roof and visceral coil darkly pigmented, often partly mottled.

Anatomy. Osphradium unpigmented, located at posterior quarter of ctenidium, narrowly oval, 0.22–0.40 mm in length. Ctenidium with 23–25 broadly triangular filaments, apices central to towards right; maximum width 0.32–0.48 mm, posterior-most filament overlapping pericaridum (rarely abutting or 2 filaments overlapping). Rectum straight in females, weakly arched in males. Renal organ extending 1/3–1/2 length of renal gland into pallial roof; renal gland 0.51–0.72 mm in length, 0.26–0.34 mm in width. Pericardium extending 1/3 of length into pallial roof. Stomach (Fig. 11A) with style sac 0.46–0.62 mm in length, stomach proper 0.49–0.62 mm in length, caecum absent to very small (up to 0.05 mm long).

Testis of 1.8–2.0 whorls; seminal vesicle visible externally and lies between digestive gland and testis for only 0.1–0.3 whorls behind stomach, convolute over stomach. Prostate gland (Fig. 12B)

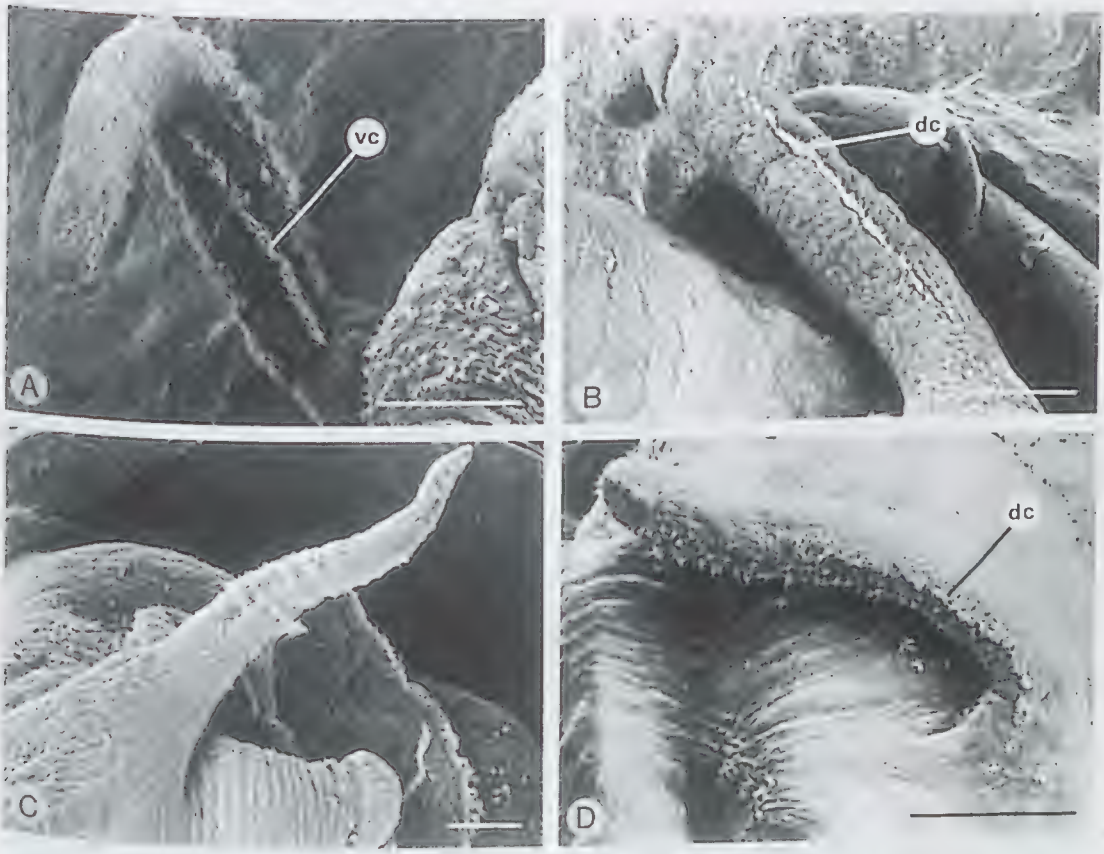

Figure 8. Cephalic tentacles of *Dalhousia* species and *Fluvidona centralia*. A,B. *D. harrisi*, Spring Ca7 (station C644), A, ventral (proximal) and laterodorsal (distal) views; B, dorsal view (also showing part of snout and foot). C. *D. globosa*, dorsal view (also showing part of snout and foot), Spring Ca1 (station 641B). D, *F. centralia*, dorsal view, Spring E1, paratype. dc – dorsal cilia; vc – ventral cilia. Scales 0.1mm.

0.42–0.43 mm in length (about 0.09–0.15 mm in pallial roof), 0.19–0.34 mm in height, broadly oval, moderately to narrowly oval in section. Pallial vas deferens undulating, unpigmented to dark grey (darker than surrounding epithelium of neck) low, rope-like ridge across neck at base of penis; a few undulations nearer prostate, straight immediately anterior to, and beneath, prostate. Penis (Fig. 13B–D) unpigmented or with proximal part of distal section of penis with grey pigmentation, basal section unpigmented or with some grey pigment; distal section long and evenly tapering, basal section relatively small, expanded. Penis base 0.35–0.38 mm from right eye, just to right of midline of head.

Ovary of 1.0–1.3 whorls. Coiled oviduct (Fig. 14B,D, co) with 1 distal U-shaped loop, orientated anteriorly to vertically; distal part arched dorsally to top of sperm sac, posteriorly, wrapped around sperm sac in S-shape coil. Duct to sperm sac anterior, very short. Common duct (Fig. 14B, cd) long, straight. Sperm sac (Fig. 14B,D, sps) globular, 0.28–0.35 mm in maximum length, 0.25–0.31 mm in maximum width. Albumen gland (Fig. 14B, ag) 0.55–0.66 mm in length, 1/7–1/4 of length in pallial roof; slightly shorter than capsule gland. Capsule gland (Fig. 14B, ag) rounded bluntly tapered anteriorly, circular to oval in section, about 0.7 mm in length, with distinct glandular zones. Ventral channel (Fig. 14B, vc) narrow, lacking distinct vestibule, small, short opening (Fig. 14B, po) at or slightly behind anterior end of capsule gland.

Distribution (Fig. 15). Found living around the water edge of the main pool of Ca1. Springs

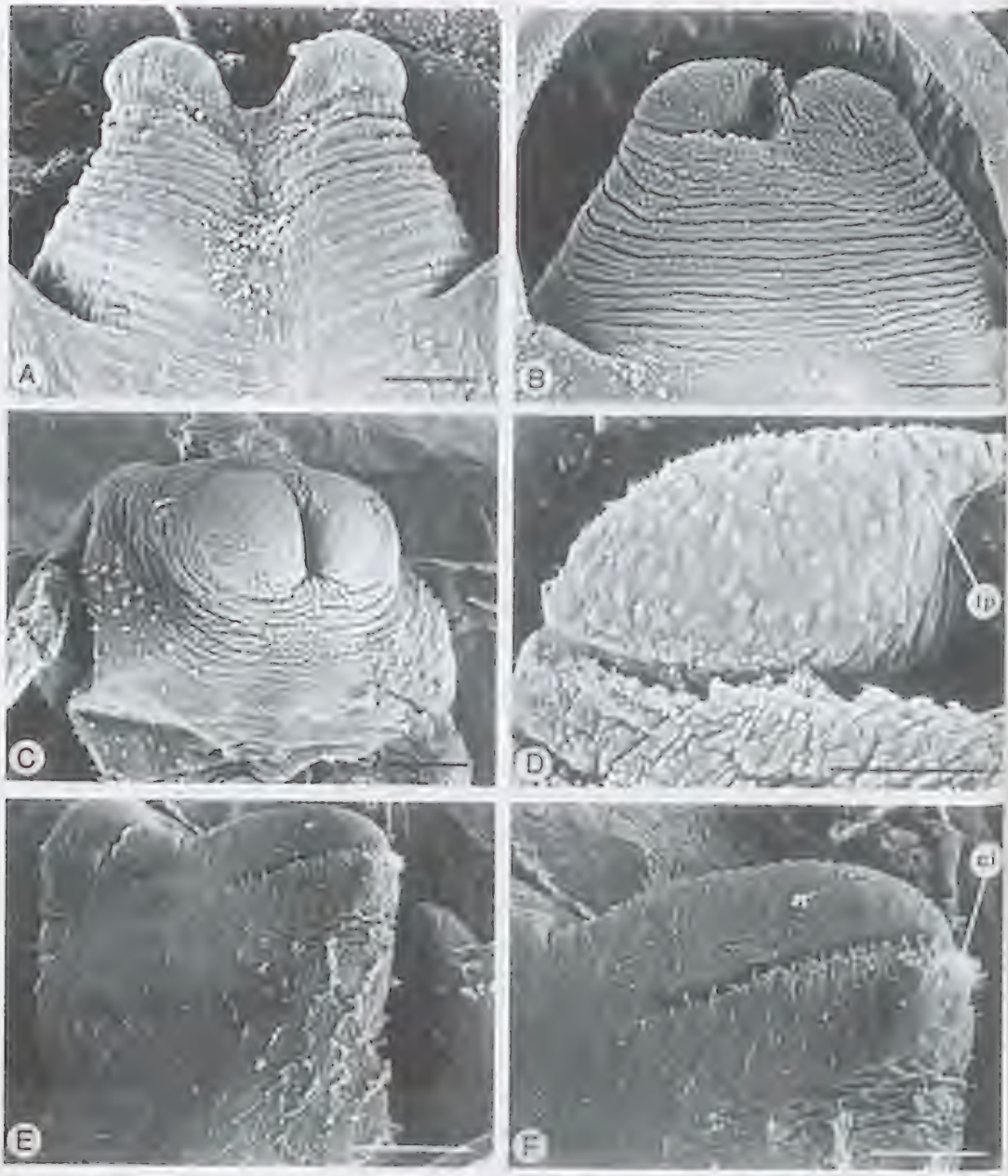

Figure 9. Snout morphology of *Dalhousia* species and *Fluvidona centralis*. A *D. glebula*, dorsal view, Spring Ca1 (station 641B). B–D *D. harrisi*, Spring Ca7 (station C644). B,D, dorsal view, D, high power view of left labium; C, ventral view. E,F *F. centralis*, paratype. Dorsal view; F, high power view of right anterior end of snout. ci – cilia, lp – labial papillae. Scales A–C,E – 0.1mm, D,F – 0.05mm.

confirmed as containing this species are listed in Table 8 (Appendix 3).

This species lives in a wide range of habitats ranging from small cold seeps (recorded temperatures of down to 20°C), to large warm pools to very hot (up to 43°C) springs. It is found in all spring groups except the Gb subgroup.

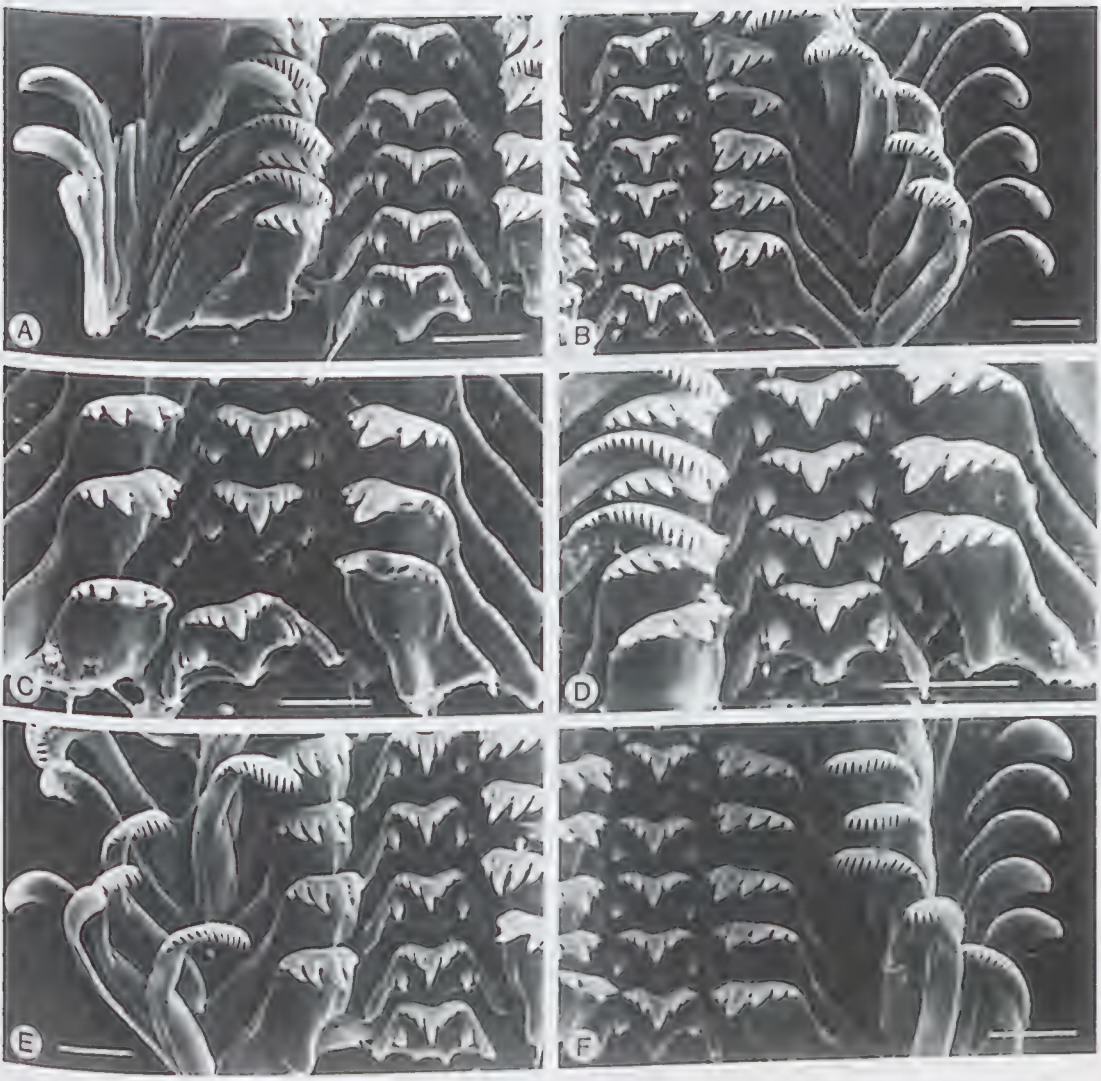

Figure 10. Radulae of *Dalhousia* species. A,E. *Dalhousia harrisi*. A, Spring Ca13A, E, Spring Ca7 (station C644). B–D,F. *D. globosa*, Spring Ca1 [station 641 (B,C) and Ca1We (D,F)]. Scales 0.02mm.

Remarks. This species is distinguishable from *D. globosa*, when in sympatry, by its generally smaller size (Fig. 16D, 22A) and taller spire. It lives in sympatry with *D. globosa* in springs Ca1, A1, A2, A8, B1, Ca8, Cc1, Cc3, and Cd1. Hybrids have been found in Ca8 and Cd2 (Appendix 3, Table 8). In Ca1 it has been found only on the edges of the large pool where it is effectively out of reach of the catfish which are known to eat hydrobiid snails (Ponder, 1989). Other than the shell characters, there are no obvious, consistent morphological synapomorphies which separate this species from *D. globosa*, although in the type population the anteriorly placed bursal duct is a consistent difference. The distribution of this character was checked in all other populations and was found to be ventrally to posteriorly placed, as in *D. globosa*. The capsule gland has more distinct glandular zones in *D. harrisi* than in *D. globosa* in most populations, but, again, this is not consistent. The genetic differences between these two taxa are summarized in the diagnosis and detailed below. Allozyme variation within this taxon is also detailed below (see also Appendix 3, Table 8).

D. harrisi is generally rather uniform in size in the northern spring groups (A and B) (Figs 16B, 16D), but varies considerably in the other spring groups (C–H) (Fig. 17). However, generally there is a considerable amount of variation in shell size and shape within this species (Appendix 2, Table 2; Figs 4, 5, 17; Ponder, 1989, figs 11.1A–E,G, 11.2A,D,E). The type population (Fig. 2A,B) is more similar to *D. globosa* in shell shape than most others (compare Figs 2A,B with 2H), although rather globose specimens are encountered in other populations (e.g. Fig. 4A,B,D). Mean shell size, in the 36 measured populations, ranges from 1.5 to 4.1 mm (Appendix 2, Table 2) with considerable variance in some populations (Table 2, Fig. 17, and compare Figs 4A,B, D; 4C,E; 4F,G; 4H,I; 5A,B; 5E,G,H), and many populations differ significantly ($P<0.001$) from conspecific populations in length and other dimensions and ratios. Overall there is a significant ($P<0.001$) difference in most shell dimensions and ratios between sexes. Comparisons with *D. globosa* show a significant ($P<0.001$) difference in all measured shell dimensions and their ratios.

Several populations of *D. harrisi* have a proportion of individuals infected with parasites. In some samples the infected individuals are significantly larger than other members of the population but in others this is not the case. Eliminating parasitized individuals does not markedly alter the patterns of variation in shell size.

Genus *Fluvidona* Iredale, 1937

Type species: *Hydrobia petterdi* Smith, 1882.

Remarks. The anatomy of the Wilson's Promontory species of this genus is described in detail by Ponder *et al.* (1994). The species described below is included in *Fluvidona* because its radular, anatomical, opercular and shell characters agree with members of that genus in most respects. There are only two significant anatomical differences between this taxon and other species of *Fluvidona*. One is the position of the bursal duct which is located at the ventral end of the anterior edge of the bursa copulatrix in most individuals, whereas it opens in the middle of the anterior edge in other species of *Fluvidona*. The second character is the long, tapering penis with a narrow (not wide) base which is not markedly set off from the distal part of the penis as in other members of the genus.

The genus name *Fluvidona* is used following Ponder *et al.* (1994) but electrophoretic studies by one of us (S.A.C., in prep.) indicate that typical *Fluvidona* from northern NSW is generically distinct from the southern species attributed to this genus.

Fluvidona centralia n. sp.

Figs 2D,E, 6C,D, 7F–H, 8D, 9E,F, 12D, 18–19–20–21, 25.

Etymology. Centralia – refers to the centre of Australia.

Type locality. Spring Cd11, Dalhousie Springs, South Australia.

Collection details of type material. Stn. D70, Spring Cd11, 26°24'40"S 135°30'29"E, small seepage on large mound, temp. 24°C, 9/5/1990, Coll. DC SC.

Holotype, SAM, 18941; paratypes, SAM, 18942; AMS, C.201748.

Diagnosis. With small, conical shell, prominent opercular pegs, 4–5 pairs of basal cusps on central teeth of radula, a ventrally located bursal duct and a narrowly tapering penis with a long, narrow base.

Description. Shell (Fig. 2D,E, 18). Shell opaque, small (1.4–2.2 mm, mean 1.8 mm), conical, SW/SL 0.56–0.67 (mean 0.62), AL/SL 0.36–0.46 (mean 0.40). Protoconch (Fig. 6C,D) of about 1.25 whorls, distinctly punctate. Teleoconch of 2.7–3.5 (mean 3.1) convex whorls, sutures moderately

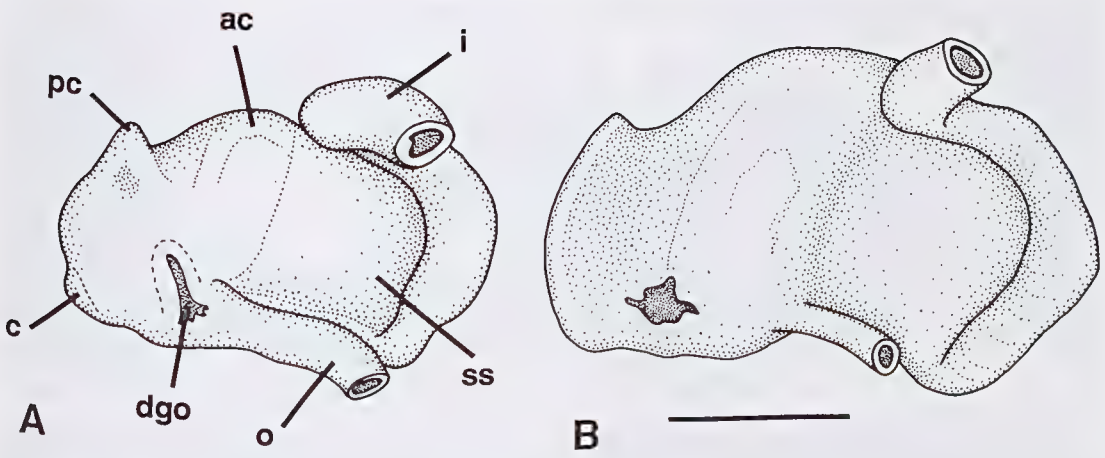

Figure 11. Stomachs of paratypes of *Dalhousia* species, viewed from the left side. A. *D. harrisi*. B. *D. globosa*. ac – anterior gastric chamber, c – caecum, dgo – digestive gland opening, i – intestine, o – oesophagus, pc – posterior gastric chamber, ss – style sac. Scale 0.5mm.

impressed; sculpture of indistinct growth lines only. Aperture usually slightly longer than wide, AW/AL 0.75–1.06 (mean 0.94), angled posteriorly. Peristome slightly thickened internally, entire, with thin inner lip attached to parietal wall; external varix absent. Colour yellow-brown to brown due to periostracum. There is no significant sexual dimorphism in shell size in the type population.

Dimensions of holotype.

	SL	SW	AL	AW	BW	TW
Holotype	2.02	1.21	0.86	0.76	1.39	3.0
Figured specimen, D62 (AMS, C.201749)	2.77	2.26	1.12	1.03	2.05	3.6

Dimensions of specimens from paratype series

Female, N=5

	SL	SW	AL	AW	BW	CV	TW
Minimum	1.72	1.03	0.69	0.68	1.29	0.11	2.7
Maximum	2.17	1.27	0.86	0.81	1.58	0.20	3.3
Mean	1.89	1.18	0.79	0.74	1.43	0.16	3.05
S.D.	0.18	0.10	0.07	0.05	0.11	0.04	0.20

Male, N=15

	SL	SW	AL	AW	BW	CV	TW
Minimum	1.47	0.89	0.60	0.55	1.07	0.10	2.7
Maximum	2.14	1.28	0.79	0.77	1.46	0.22	3.5
Mean	1.79	1.10	0.71	0.66	1.30	0.16	3.09
S.D.	0.20	0.11	0.07	0.06	0.11	0.03	0.22

A summary of the shell measurements of additional populations of this species are given in Appendix 2, Table 3.

Operculum (Fig. 7F–H). Ovate, thin, pale yellow, with eccentric nucleus, with 1–4 well-developed pegs emerging from white smear on inner side.

Statistics of 20 opercula from the type series.

Female, N=5

	OL	OS	PL	PH	PN
Minimum	0.67	0.11	0.08	0.04	2
Maximum	0.82	0.24	0.16	0.11	4
Mean	0.76	0.18	0.11	0.07	3
S.D.	0.06	0.05	0.03	0.03	0.71

Male, N=15

	OL	OS	PL	PH	PN
Minimum	0.62	0.11	0.04	0.03	1
Maximum	0.82	0.25	0.19	0.18	4
Mean	0.71	0.17	0.10	0.09	2.93
S.D.	0.06	0.04	0.04	0.05	0.96

Radula (Fig. 19). Central teeth broad, each with 4–6 (usually 5) small, triangular cusps on either side of a sharp median cusp about twice the length of the adjacent cusps. 3–4 pairs of lateral basal denticles present, innermost larger. Lateral teeth with largest cusps in tooth row, 4–5 on inner side of

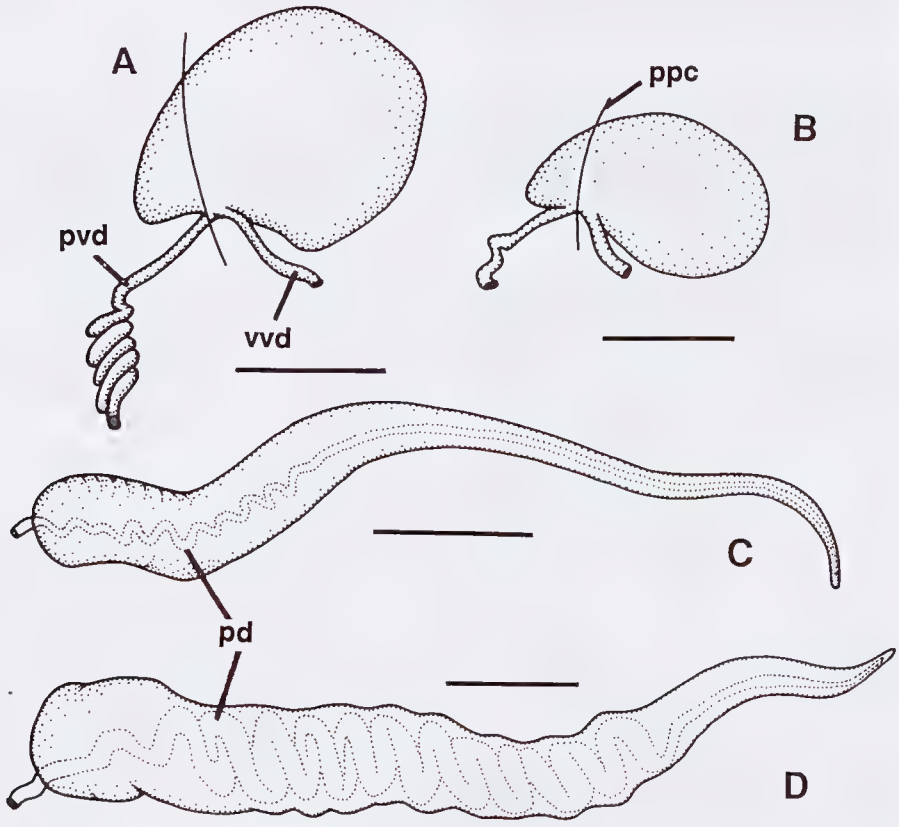

Figure 12. Male genitalia of paratypes of *Dalhousia* species and *Fluvidona centralia*. A. Prostate gland of *Dalhousia globosa* viewed from left side. B. Prostate gland of *Dalhousia harrisi* viewed from left side. C. Penis of *Dalhousia globosa*. D. Penis of *Fluvidona centralia*. pd – penial duct, ppc – posterior end of pallial cavity, pvd – pallial vas deferens, vvd – visceral vas deferens. Scales A,B – 0.25mm, C – 0.5mm, D – 0.1mm.

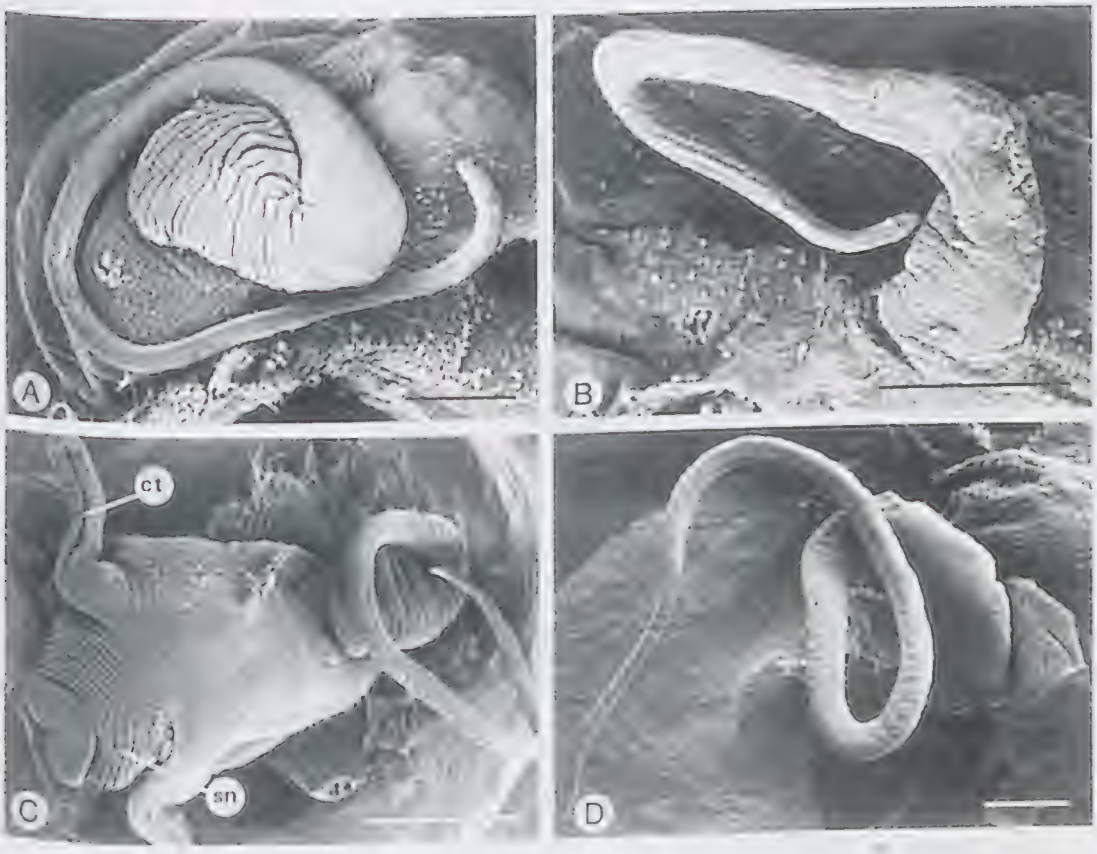

Figure 13. Head and penes of *Dalhousia* species. A. penis of *D. globosa*, Spring Ca1 (station C641B). B, D. Penes of *D. harrisi*, B, Spring Ca7 (station C644); D, Spring Ca1 (station C641A). C. Head and penis of *D. harrisi*, Spring Ca1 (station C641A). ct – cephalic tentacle; sn – snout. Scales A,B,D – 0.2mm, C – 0.5mm.

large triangular median cusp and 4–6 (usually 5 or 6) on outer side. Inner marginal teeth with 25–27 narrow, sharp cusps on antero-distal and outer-distal edge. Outer marginal teeth with 27–33 small, narrow, sharp cusps (approx. half length of those on inner marginal teeth) on antero-distal and inner-distal edge. (Description based on 4 radulae).

Head-foot. Animal unpigmented except for pigment patches on head behind eyes and mid-dorsally; opercular lobe usually unpigmented, rarely with trace of pigment. Ciliation on snout (Fig. 9E,F) well developed laterally, a narrow, but well-developed band laterally and latero-dorsally just behind labia, and scattered cilia dorsally. Cephalic tentacles with well-developed dorsal band of cilia (Fig. 8D) which extends most of length of tentacle, and a pair of weaker ventro-lateral bands.

Anatomy. Osphradium unpigmented, located just behind middle of ctenidium. Ctenidium with 14–16 broadly triangular filaments, apices near right side (0.06–0.15 mm from left side, maximum width 0.12–0.17 mm; abuting (or one filament overlapping) pericardium. Rectum with small to moderate U-shaped bend. Renal organ extending 1/3 to 1/2 of length into pallial roof; renal gland 0.31–0.39 mm in length, 0.17–0.20 mm in width. Pericardium extending about 1/2 of length into pallial roof. Stomach (Fig. 20D) with style sac 0.32–0.43 mm in length, stomach proper 0.39–0.46 mm in length. Gastric caecum small to minute (0.01–0.20 mm in length).

Testis of 1.0–1.2 whorls; seminal vesicle beneath half whorl of testis behind stomach, moderately to markedly convolute over stomach. Prostate gland 0.31–0.32 mm in length (about half in pallial

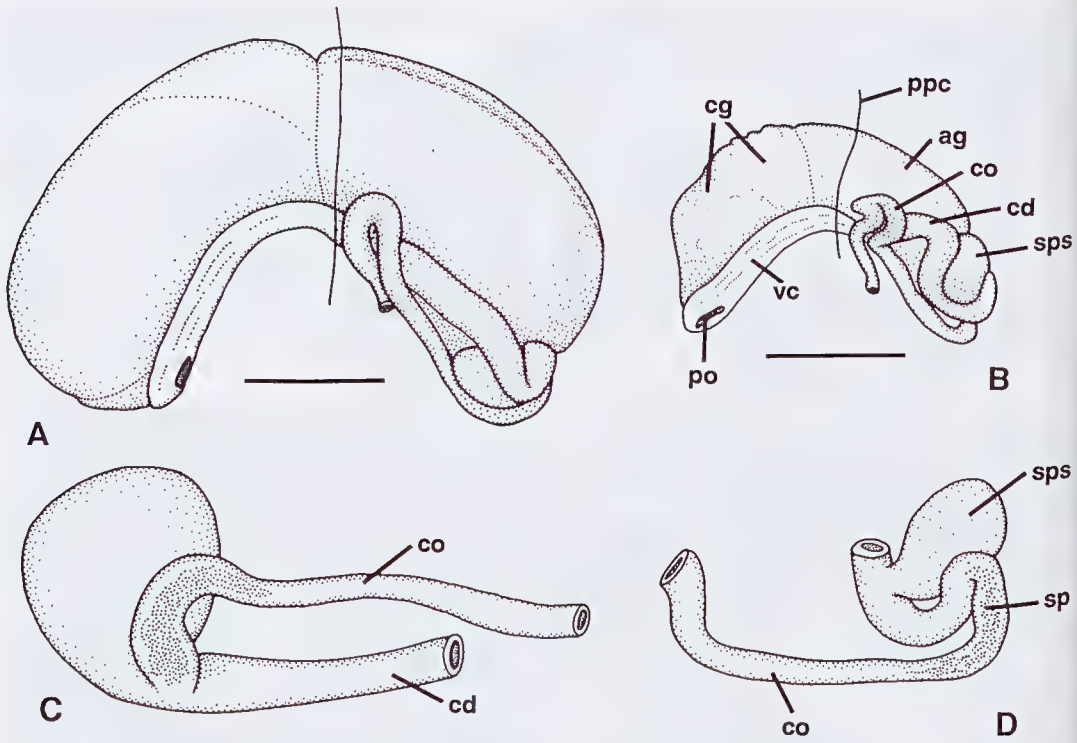

Figure 14. Female reproductive systems of paratypes of *Dalhousia* species. A,C. *D. globosa*. A, oviduct viewed from left side; C, detail of sperm sac and associated oviduct. B,D. *D. harrisi*, B, oviduct viewed from left side; D, detail of sperm sac and associated oviduct. ag – albumen gland, cd – common duct, cg – capsule gland, co – coiled oviduct, po – pallial opening of oviduct, ppc – posterior pallial wall, sp – sperm stored in oviduct, sps – sperm sac, vc – ventral channel. Scales (A,B) 0.5mm.

roof), bean-shaped, oval to narrowly-oval in section. Pallial vas deferens emerges ventrally from posterior end of pallial portion of prostate gland, straight until near penis where it weakly undulates. Penis (Fig. 12D) unpigmented, distal part short, narrow, tapering, tapers gradually into long, narrow, slightly tapering base. Penial duct strongly undulating in base, straight in distal section. Penis located just to right of midline, 0.19–0.25 mm behind right eye.

Ovary of 0.6–0.9 whorls. Coiled oviduct (Fig. 20A,B, co) with double loop, anterior U-shape bent anteriorly and posterior loop, details variable (c.f. Fig. 20A and B); distal part with weak elbow just before opening ventrally to bursal duct well behind posterior pallial wall (Fig. 20C). Common duct (Fig. 20C, cd) straight to pallial wall. Seminal receptacle (Fig 20C, sr) ovoid, 0.08–0.12 mm in length, 0.01–0.08 mm in width, at anterior edge of bursa; duct short. Bursa copulatrix (Fig. 20A–C, bc) ovoid to elongate-ovoid, (0.14-)0.29 mm in maximum length and width; bursal duct simple, 0.06–0.08 mm long, emerging from antero-ventral face (more nearly mid anterior in one specimen). Albumen gland (Fig. 20A,B, ag) 0.19–0.31 mm in length, 1/6–1/4 of length in pallial roof; length relative to capsule gland variable (0.5 to 1.12) (c.f. Figs 20A and B). Capsule gland (Fig. 20A,B, cg) truncated anteriorly, 0.26–0.37 mm in length, oval to narrowly oval in section. Ventral channel (Fig. 20A,B, vc) broad, lacking distinct vestibule, short, slit-like opening (Fig. 20A,B, po) beneath anterior end of capsule gland.

Distribution (Fig. 15). Springs known to contain this species are listed in Table 9 (Appendix 3).

This species lives in a few small (mainly cold) seeps, and in the shallow, lower outflow of at least

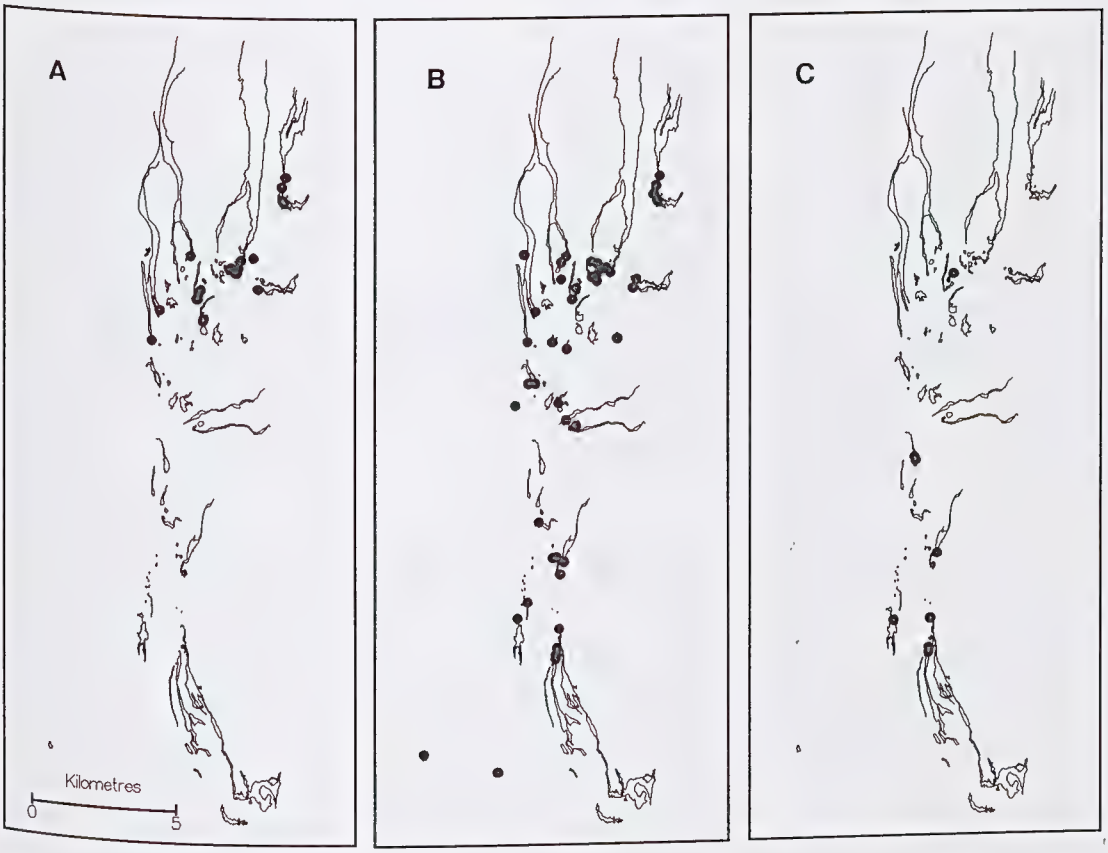

Figure 15. Distribution of *Dalhousia* species and *Fluvidona centralia*. A. *D. globosa*. B. *D. harrisi*. C. *F. centralia*.

one of the large springs. It has not been found living in sympatry with *Dalhousia*.

Remarks. This species is readily distinguished from the somewhat similar forms of *D. harrisi* with small, conical shells in having a more evenly conical spire outline. In addition, *F. centralia* differs from both species of *Dalhousia* in having more prominent opercular pegs, multiple (not two) basal denticles on the central teeth and there are considerable differences in the female genital system (compare Figs 14 and 20) and penial morphology (compare Fig. 12C,D).

Apart from the type population, a sample from a lower, cold outflow from a large spring (E1, stn. D62) was also examined in detail but proved (unlike the type population) to be heavily parasitised. The external features of the animal show the same ciliation patterns but the opercula differ in having more numerous pegs (2–7, mean 4.2) than the Cd11 sample. Radulae also differed, having fewer cusps (4–5, usually 4 on each side of median cusp on central teeth; 4 on inner side of lateral teeth and 4–5 on outer side; 18–21 cusps on inner marginals and 26–32 on outer marginals). Unfortunately most of the other samples contained insufficient material for detailed analysis so the range of variation within most populations of this taxon has not been adequately ascertained. Given the differences between the Cd11 and E1 populations, further work may well show that subdivision of this taxon is possible and this is also suggested by the level of genetic variation within the taxon (described below). In addition, given the nature of the localities frequented by this taxon, it is undoubtedly under represented in our sampling. The small seepages are often difficult to locate due to the dense vegetation and can be very easily missed. In addition, sampling the cold outflows of the

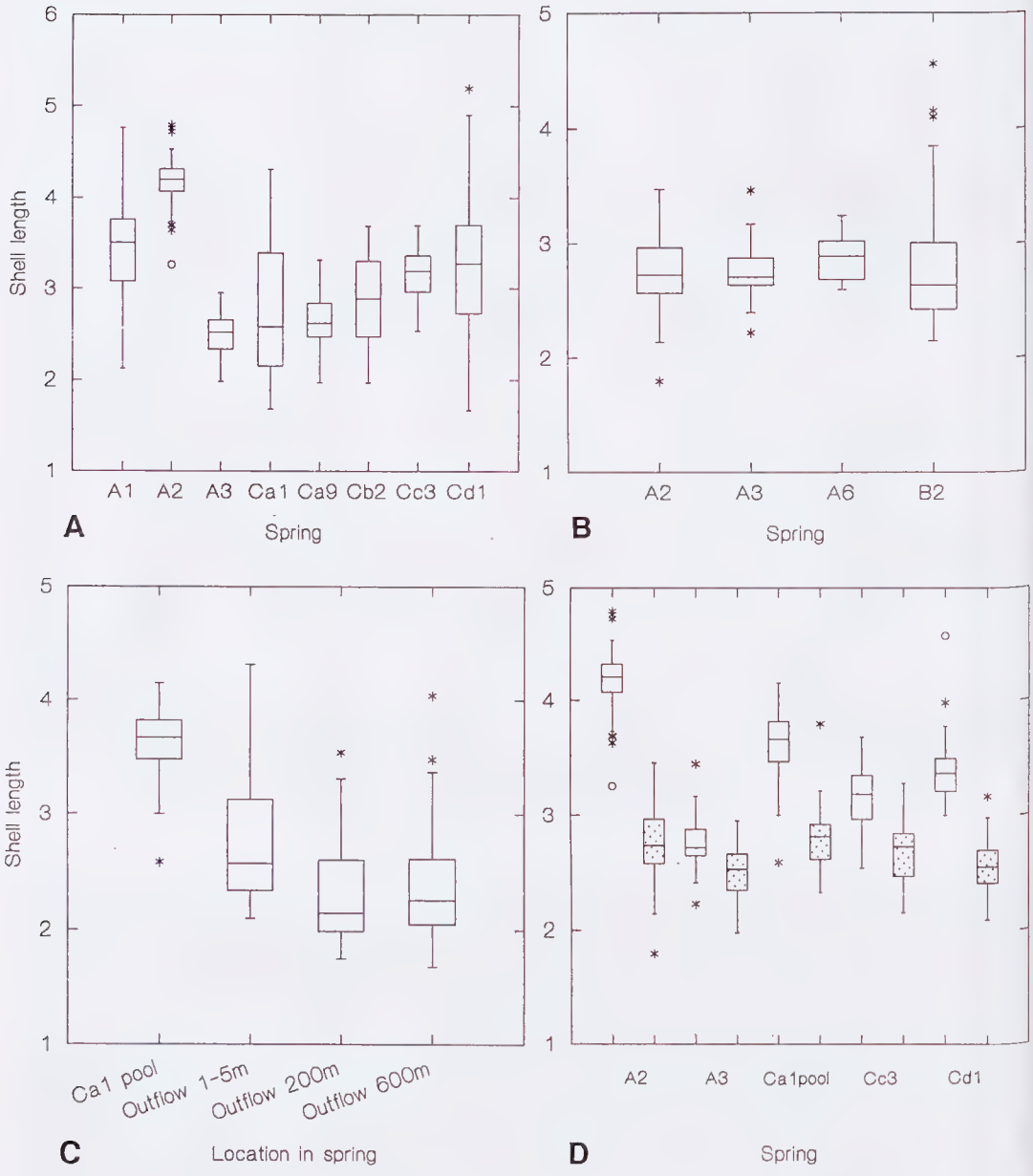

Figure 16. Box plots showing variation in shell length in *Dalhousia globosa* and *D. harrisi*. A. Shell lengths of *D. globosa*. Note that the data for Ca1 are pooled from the samples shown separately in C. B. *D. harrisi* showing variation in shell size in the A and B spring groups. C. *D. globosa*, showing variation in shell size in different sites in Spring Ca1. D. Comparison of shell lengths of *Dalhousia globosa* and *D. harrisi* (stippled) in some of the springs in which they are sympatric. The median (the mid-point of the ordered numbers) is marked inside the box, the ends of the boxes splitting the ordered numbers in half again. Outliers are represented by an asterick and extreme outliers by a circle.

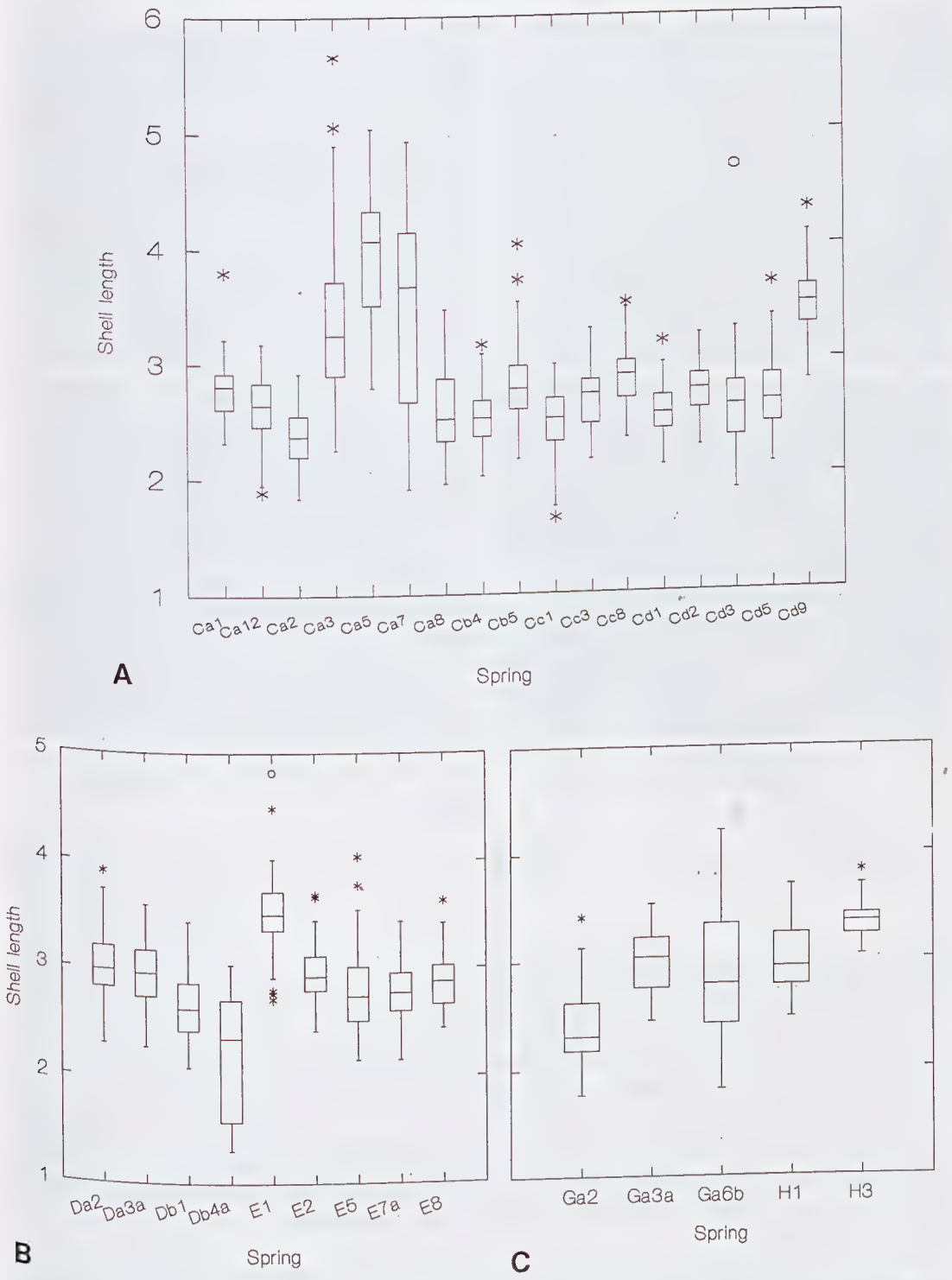

Figure 17. Box plots showing variation in shell length of *Dalhousia harrisi*. A. The C–group springs. B. The D and E–group springs. C. The G and H–group springs. For an explanation of box plots see Figure 16.

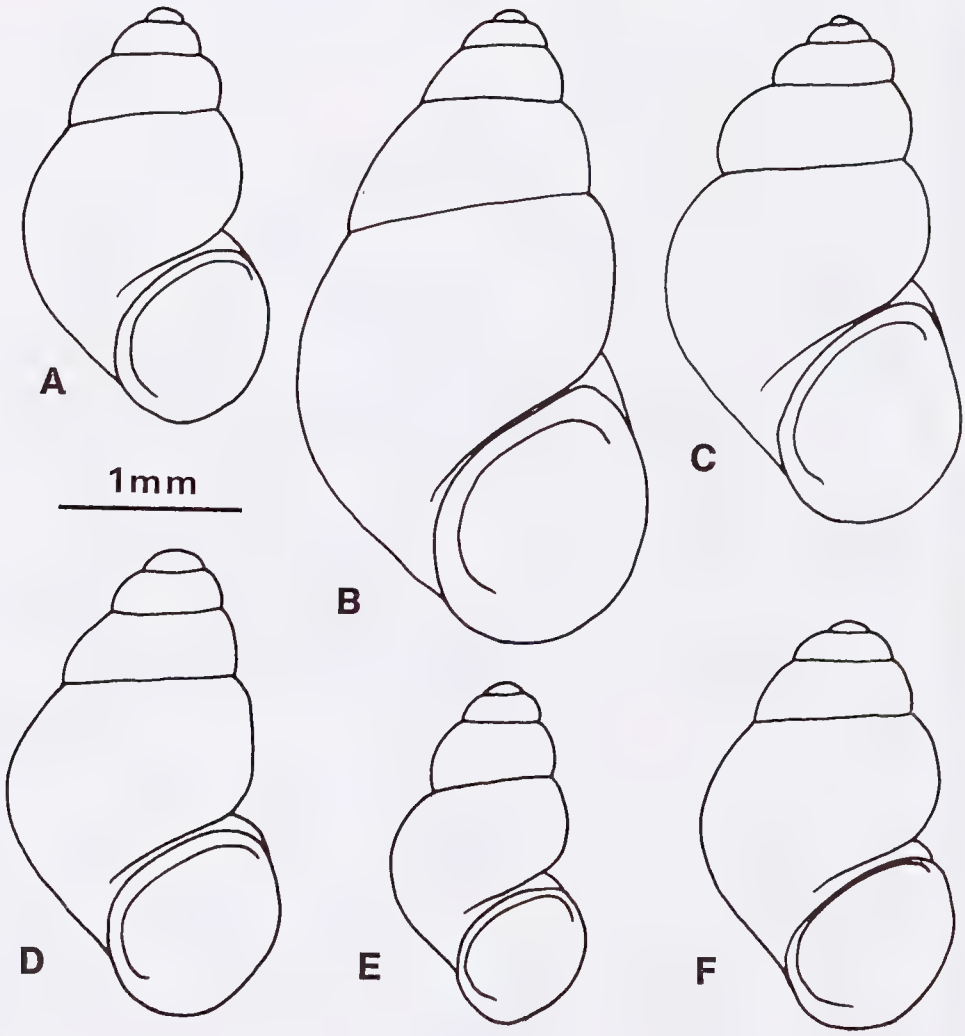

Figure 18. Shells of *Fluvidona centralia*. A. Spring Ga1 (station D13), B. Spring Ga2 (station D5), C. Spring F9 (station D53), D. Spring E3 (station D23A), E. Spring Cd11 (station D70; paratype), F. Spring Ga6A (station D15).

large springs is also difficult because of the dense vegetation and the snails, in this type of habitat, are usually very infrequent. Shell variation between populations is shown in Fig. 18.

The genus *Jardinella* (see Ponder and Clark, 1990) found in artesian springs in western Queensland, as well as in some coastal rivers in north Queensland (Ponder, 1991) is similar to *Fluvidona* in having a small seminal receptacle and large bursa copulatrix but differs in having, like *Dalhousia* and *Fonscochlea*, only two pairs of basal denticles on the central radular teeth and weak opercular pegs.

The new species represents a major range extension for *Fluvidona*, a predominantly south eastern Australian group, although undescribed taxa are known from the Flinders Ranges, as well as more coastal areas in South Australia. As noted above, the new species differs from any of the named taxa

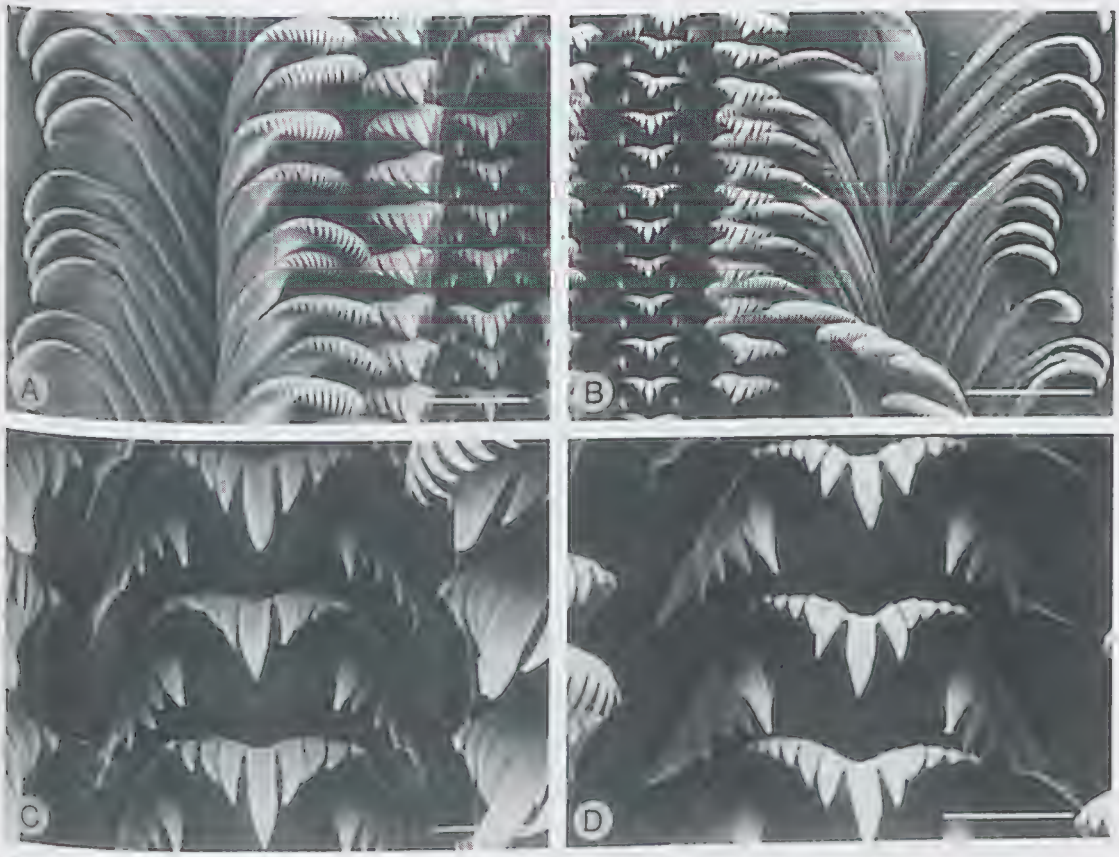

Figure 19. Radulae of *Fluvidona centralia*. A,C. Spring E1 (station D62). C, detail of central teeth. B,D. Paratype, Spring Cd11 (station D70), D, detail of central teeth. Scales A,B – 0.02mm, C,D – 0.005mm.

in having the bursal duct opening antero-ventrally to the bursa and in having a gradually tapering penis with a narrow base.

Allozyme electrophoresis.

Gene frequency tables are given for the three taxa in Appendix 3. Our results confirm that the snails are grouped into two lineages, *Dalhousia* and *Fluvidona*. *Dalhousia* is the dominant component and is widespread throughout the Dalhousie Spring system. The second group was found in only seven localities, predominantly in the small seepages and in the lower, swampy outflow from a large spring (E1). Allozyme mobilities and activities differ so much between these two groups that no evolutionary relation between them can be discerned. Consequently, the allozymes within each group were named and analysed separately.

Dalhousia can be sub-divided into at least two genetic species recognised on the basis of characteristic suites of allozymes. *D. globosa* is characterised by very high frequencies of the *Lap* 2, *Pgm-2* 3, *Sdh-1* 1 and *Sdh-2* 2 alleles, and a high frequency of the *Gpi* 2 allele. These allozymes are virtually absent or found in very low frequencies in *D. harrisi* which is characterised by high frequencies of *Lap* 3 and *Pgm-1* 4, which are virtually absent in *D. globosa*, *Sdh-1* 2 and *Sdh-2* 1. With the exception of samples from Ca8 and Cd2 springs, where there appears to be a breakdown of isolating mechanisms, there were very few heterozygotes at the *Lap* or *Pgm* loci which comprised a characteristic allele from each of *D. harrisi* and *D. globosa*. Individual snails were scored and

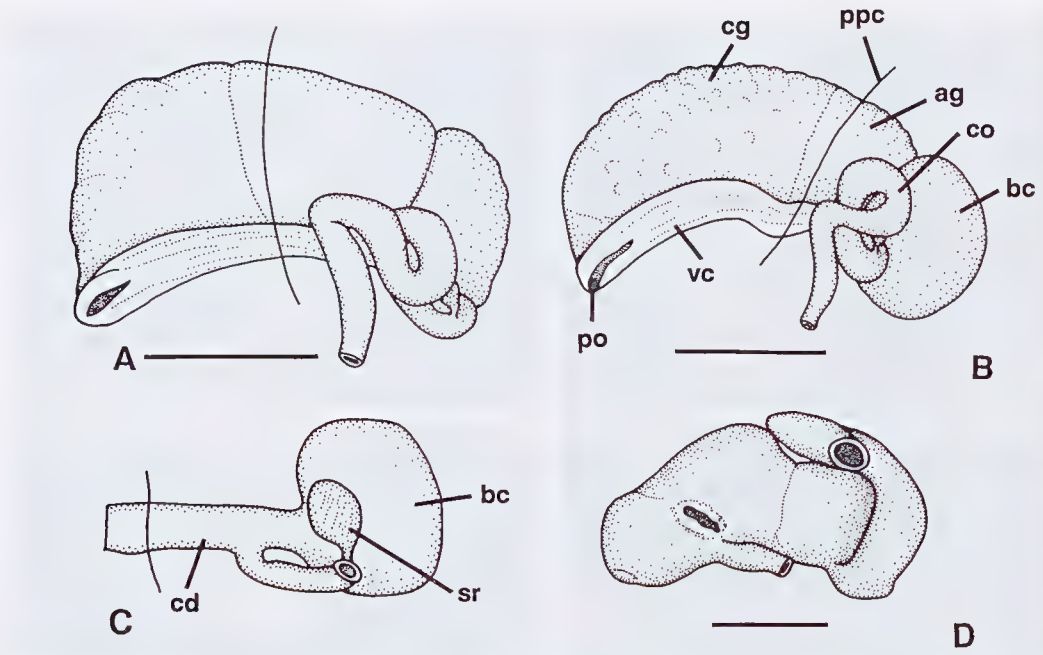

Figure 20. Female reproductive system and stomach of *Fluvidona centralia*. A,B. Oviducts of two paratypes viewed from the left side, showing variation in coiling pattern of coiled oviduct and relative length of albumen gland. C. Detail of bursa copulatrix, seminal receptacle and associated ducts from left side. D. Stomach from left side (see Figure 8 for labels). ag – albumen gland, bc – bursa copulatrix, cd – common duct, cg – capsule gland, co – coiled oviduct, po – pallial opening of oviduct, ppc – posterior pallial wall, sr – seminal receptacle, vc – ventral channel. Scales 0.25mm.

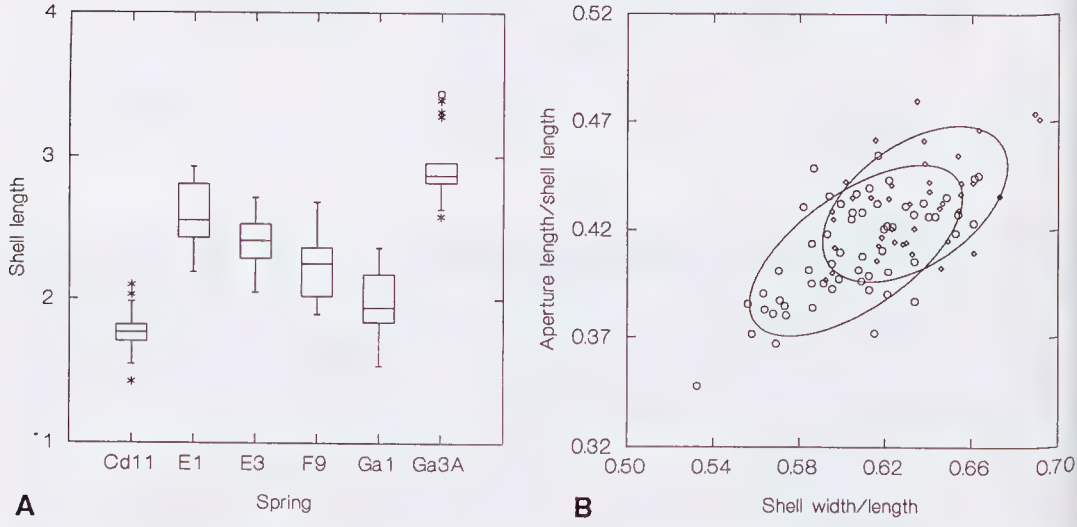

Figure 21. A. Box plots showing variation in shell length of *Fluvidona centralia* (For an explanation of box plots see Figure 16). B. Separation of the two electrophoretically distinct groups within *F. centralia* using two shell ratios. Samples from springs Cd11, E1 and F9 are represented by circles, those from springs E3 and Ga1 by diamonds. The ellipse represents 75% of the variance.

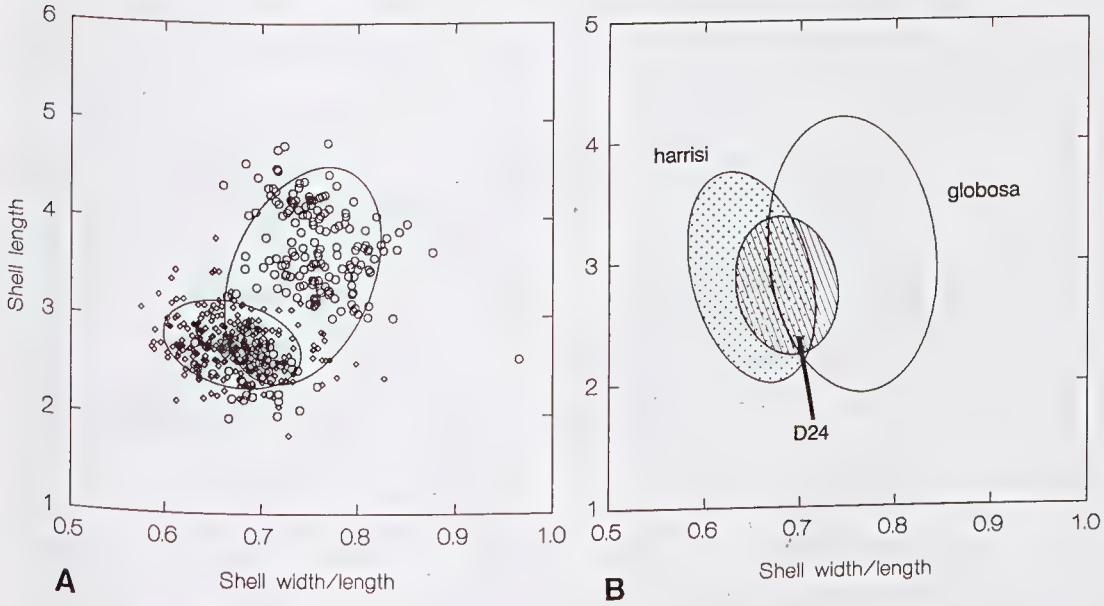

Figure 22. A. Plot of shell length and the ratio of shell width/length for sympatric populations of *Dalhousia globosa* (circles) and *D. harrisi* (diamonds). B. Plot of shell length and the ratio of shell width/length for all measured populations of *Dalhousia globosa* (except station D24), Cala (station D24) and *D. harrisi*. The ellipses in both figures contain 75% of the variance. The individual data points have not been plotted in B.

allocated to one of these genetic species on the basis of their allelic constitution for these loci. In springs Ca8 and Cd2, snails were allocated to *D. globosa* if they were homozygous for *Lap* 2, to *D. harrisi* if they were homozygous for *Lap* 3, and to a "hybrid" category if they were 2/3 heterozygotes. A number of other allozymes have distributions correlated with the genetic species (Tables 7,8). Two are restricted to *D. globosa* and 12 to *D. harrisi*. No individual in any spring was identified as a potential F_1 hybrid so that the genetic isolation between the species is nearly complete. When individuals are allocated to genetic species and samples pooled within spring groups there is a complete separation of *D. globosa* and *D. harrisi* in phenetic trees (Figs 23, 24).

Summaries of genetic variation within samples are given in Tables 4–6, which detail the average number of individuals scored per locus, the percentage of loci with more than one allele and observed and expected heterozygosity. These summaries show a notable level of genetic variation in *Dalhousia*, with most samples having multiple alleles at more than 20% of loci. The *D. globosa* sample from the Ca1 pool (topotypic population) has multiple alleles at 53% of loci. Some samples with low variability are intriguing. Ca8 is one of the two springs where there is evidence of significant hybridization between *D. globosa* and *D. harrisi*. Yet it has the lowest percentage of polymorphic loci among the populations of *D. globosa* and one of the lowest seen in *D. harrisi*, accompanied by a low value in the "hybrids" class. Polymorphic loci are quite frequent in Cd2, the other spring where hybridization is occurring.

The genetic isolation between *D. globosa* and *D. harrisi* is emphasised by their wide sympatry within the springs. This criterion is not available for decisions regarding the specific status of lineages within the two nominate genetic species. Of particular interest here, is the population in a hot spring near Ca1, Cala (stn D24). This is an outlier to the other samples of *D. globosa* in phenograms (Figs 23, 24), principally because of a very high frequency of ALKP 3, LGG-2 2, SDH-1 2 and SDH-2 1 allozymes and the fixation of an unique GAL allozyme (3). The SDH phenotype is similar to *D. harrisi*. The three other characteristic allozymes of this hot spring population are absent or in very low frequencies in *D. harrisi*, contradicting a hybrid origin. It appears more likely that the

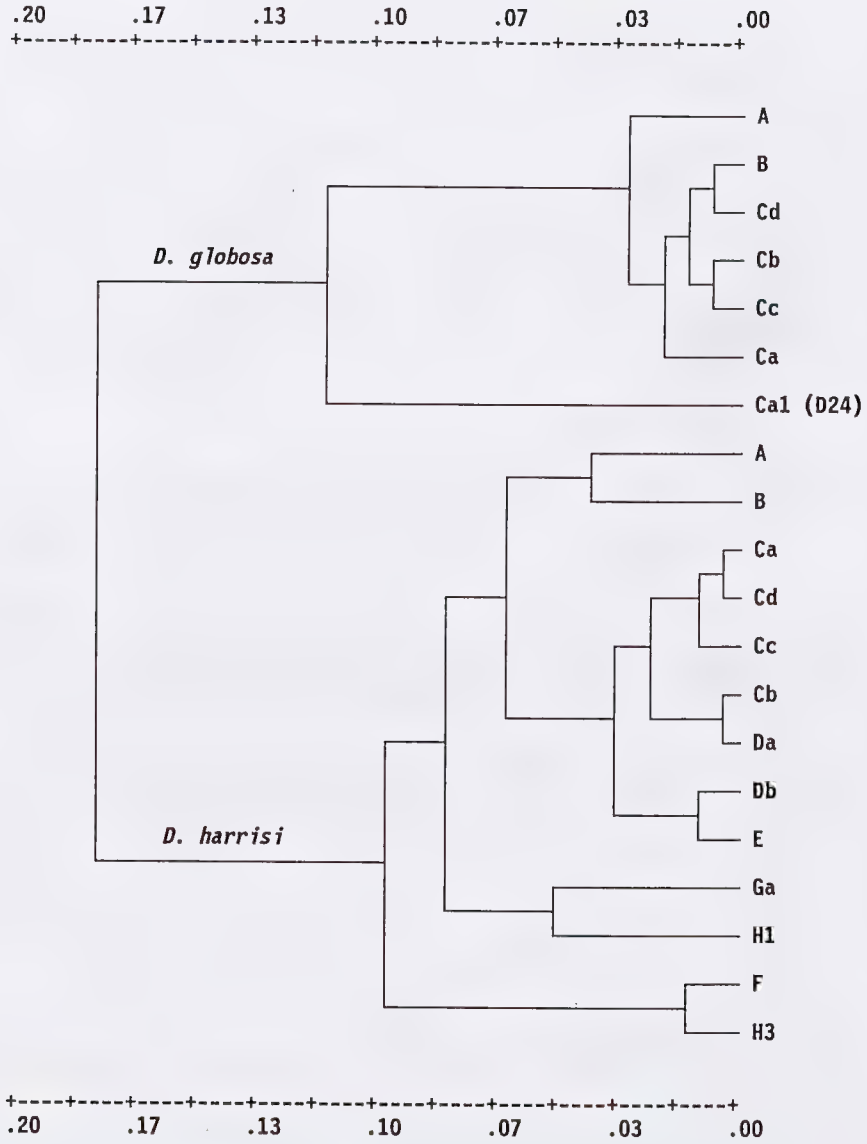

Figure 23. Phenogram showing relationships of *Dalhousia* based on unweighted pair group (UPGMA) clustering of Nei's unbiased (Nei, 1978) genetic distances between samples pooled into spring groups. *D. globosa* Cala (D24) and *D. harrisi* H1 and H3 samples have been treated separately, as suggested by inspection of their genetic frequencies.

Ð24 population has been sufficiently isolated from *D. globosa* populations for long enough to evolve large allelic frequency differences and, in at least this one example, novel allozymes. This population has the shell features of *D. harrisi* (Fig. 3E,H), there being no significant ($P<0.01$) differences in shell dimensions and ratios. However, members of this sample tend to fall in the overlap zone between the two species (Fig. 22B).

Figure 23 shows that the distribution of genetic variation in *Dalhousia* is not random. The genetic distance between populations pooled in spring groups is generally concordant with the degree of

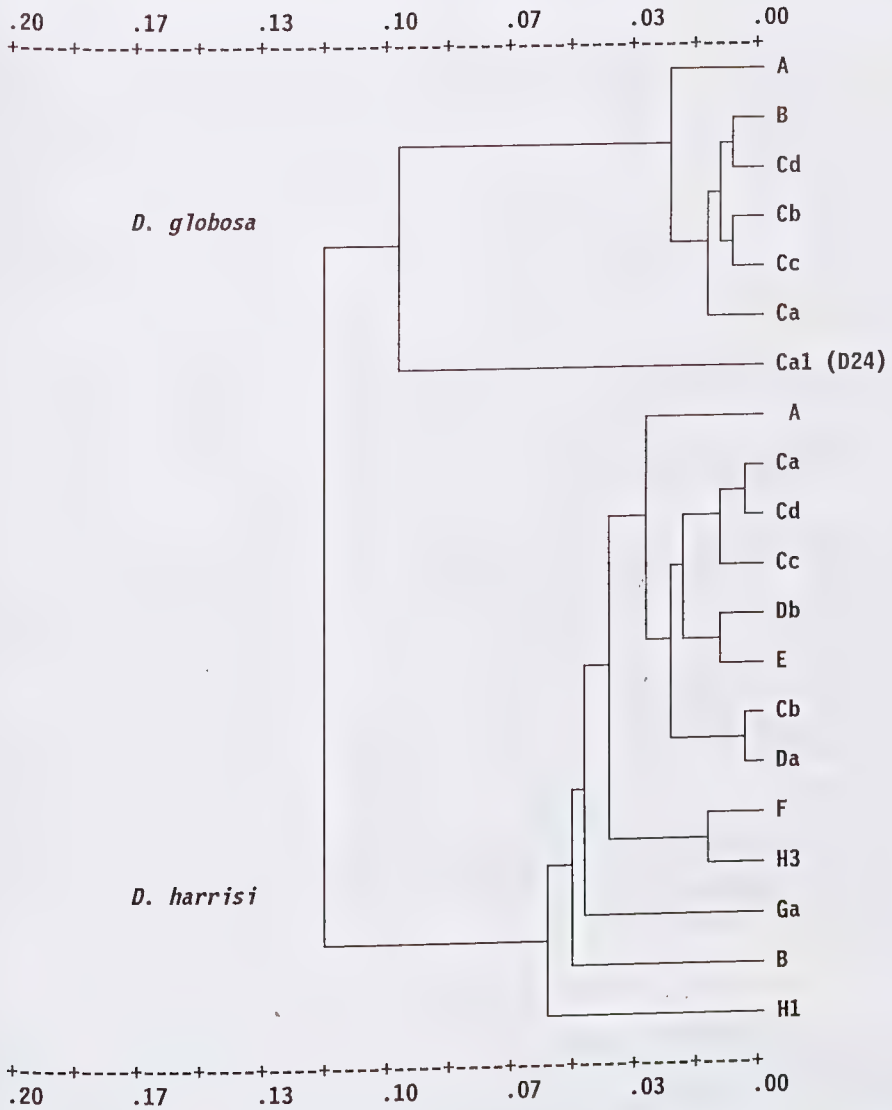

Figure 24. Phenogram showing relationships of *Dalhousia* based on complete linkage clustering of Nei's unbiased (Nei, 1978) genetic distances between samples pooled into spring groups. *D. globosa* Ca1a (D24) and *D. harrisi* H1 and H3 samples have been treated separately, as suggested by inspection of their genetic frequencies.

geographic separation, particularly in *D. harrisi*. Clear exceptions to this are the high degree of divergence of the Ca1a (D24) sample from the remainder of *D. globosa* and the low divergence between the F spring group and the geographically distant H3 spring in *D. harrisi*. In *D. harrisi*, spring group B is quite basal when UPGMA linkage is used for the clustering (Fig. 23). If, however, the phenogram is based on "complete" linkages, the pooled sample for B is the sister to A (Fig. 24). Phenograms (*e.g.* Fig. 23) reveal a number of lineages in *D. harrisi* characterised by frequency differences from other lineages within the species. Whilst there are no examples of fixed allozymic differences, some polymorphic loci have allozymes restricted to particular geographic areas. The prime example is the ß-GAL 1 allozyme which is, with the exception of low frequencies in A1 and A2, found in the southern and southeastern springs. Other instances include the LGG-1 2 allozyme

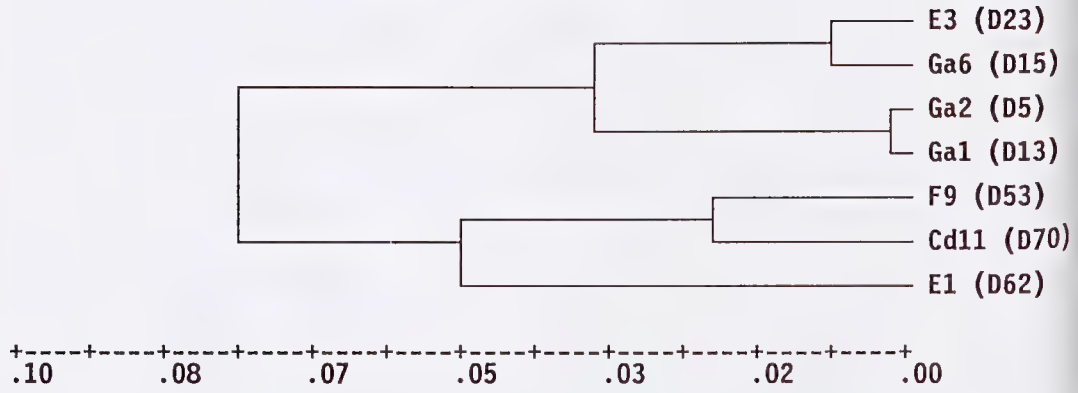

Figure 25. Phenogram showing relationships between populations of *Fluvidona centralia* based on an unweighted pair group (UPGMA) clustering of Nei's unbaised (Nei, 1978) genetic distances.

which is usually absent from the C and D spring groups, the ADH 4 allozyme with a disjunct distribution in groups A and H and the HK 3 allozyme concentrated in B and the adjacent Db groups.

Sample sizes are small in *F. centralia*, yet the apparent low levels of variation in this species (Table 6) probably reflect its biology, implying smaller founding populations and longer periods of isolation than in *Dalhousia*. There are two principal lineages within the species (Fig. 25), these characterised by a fixed-difference in *Gpt-2*. This may reflect a significant biological division or geographic variation within the the taxon as we recognise it. There are no other allozymes with distributions concordant with the *Gpt-2* pattern although there are some loci (such as *Pgd*) with allozymes found only in some populations of one of the two lineages. The shell morphologies (Fig. 18; Table 3) of members of these two lineages do not differ greatly, there being no significant differences between any of the measurements for the pooled measured populations listed in each group. However, the ratios of shell width/shell length and aperture length/shell length were significantly different ($P<0.001$; Fig. 21B) between the two groups for the subset of measured populations.

Discussion

Using the criterion of sympatry, we have recognised only two species-group taxa within *Dalhousia*. However, as outlined above, some of the lineages within both these species are genetically distinct, although allopatric, and both taxa show considerable intra and interpopulation variation in shell size and shape. Similarly within what we treat as a single species of *Fluvidona* there is considerable interpopulation variation in shell, opercular and radular morphology, as well as allopatric genetic subdivision.

The considerable variation seen in shell morphology in *Dalhousia* (Figs 2–5, 16, 17), briefly described above, will be analysed in more detail elsewhere.

As noted above, it is very likely that *Dalhousia* and *Fonscochlea*, from the Lake Eyre Supergroup, are sister taxa. The probable sister taxon to (*Fonscochlea* + *Dalhousia*) is *Jardinella* (Ponder and Clark, 1990), found in artesian springs in western Queensland, as well as in some coastal drainages in northern Queensland. Species of *Jardinella*, like most hydrobiids, have a normal bursa copulatrix and seminal receptacle. The presence of a single sperm sac (presumably the bursa copulatrix) in *Dalhousia* might appear to suggest that it is more derived than *Fonscochlea* which has two. However, the two sperm sacs of *Fonscochlea* are very similar histologically and may be the result of subdivision of an original single sperm sac (the bursa) (Ponder *et al.*, 1989). If this is the case, in this respect at least, *Dalhousia* is the more plesiomorphic of the two genera and in this genus the oviduct functions as a sperm storage site.

The presence of an endemic hydrobiid genus at Dalhousie Springs with a sister group in the Lake Eyre Springs raises questions about the origin and age of these taxa. Unfortunately there are few concrete data on the age of any of the springs associated with the Great Artesian Basin. The age of Dalhousie Springs has been discussed by Krieg (1989) who concludes that they are probably Pleistocene in age, being no older than 1–2 million years. Ponder (1986) has suggested that the Lake Eyre Supergroup springs contain such a differentiated fauna that they may well be Tertiary in age. If Dalhousie Springs are indeed Pleistocene in age, it is highly probable that *Dalhousia* is an immigrant to the springs from some other, now extinct, artesian spring group. It is possible (although unlikely), that *D. globosa* and *D. harrisi* had become specifically distinct before this immigration. Thus, in this scenario, the *Dalhousia* fauna of Dalhousie Springs would represent two colonization events. The presence of *F. centralia* indicates that multiple invasions of hydrobiids are possible and, indeed, cannot be discounted from our genetic data. The genetic differentiation of the D24 population from other samples of *D. globosa* has probably developed *in situ*, although, again, the possibility of a third colonization cannot be discounted. The genetic distance between D24 and *D. globosa* is comparable to that between *D. globosa* and *D. harrisi*, supporting the idea that there has been sufficiently long residence of *Dalhousia* at Dalhousie Springs for speciation to have occurred *in situ*.

The ancestry of *Fluvidona*, on the other hand, is probably not tied to artesian springs and this species may be an immigrant from some, probably now extinct habitat, or, possibly, the Flinders Ranges. It seems to us, however, that recent dispersal of such faunas between these two widely separated areas is less likely than immigration of the hydrobiids from nearby, previously suitable habitats, possibly in the early Pleistocene.

The phreatic amphipod at Dalhousie (Zeidler, 1991) is related to another surface species living in the springs, so may have evolved *in situ*. On the other hand, the surface amphipod (*Austrochiltonia* sp.) is similar to a species living in the Lake Eyre Supergroup springs and in many other aquatic habitats in southern Australia (Zeidler, 1989), although it is not known elsewhere in central Australia, except Edgbaston Springs in western Queensland (Ponder, 1986).

The evolution of the hydrobiids within Dalhousie Springs will be discussed in more detail elsewhere. Their great morphological plasticity may in part be coupled with their considerable genetic diversity. The interplay of factors in the physical and biological environment may also have a significant influence on shell morphology. There is a considerable range of physical factors such as spring size, water depth and temperature and biological factors are also probably important. Ponder (1989) suggested, for example, that the presence of the predatory catfish (*Neosilurus* sp.) in some of the large springs may result in the selection of larger, heavier-shelled individuals. Other biological factors, such as parasitism, can be significant in some springs.

Dalhousia globosa and *D. harrisi* maintain their genetic integrity over their range within the spring groups, clearly indicating that they are distinct species. Each may yet be found to represent a species complex, with the Cala (D24) sample of "*D. globosa*" being the most likely candidate. It may be noted, however, that gene flow in both *D. globosa* and *D. harrisi* is apparently high when pooled data are considered, with spring groups exchanging migrants at rates of the order of 20 individuals per spring group per generation (Colgan & Ponder, 1994). This level of gene flow would generally be sufficient to prevent fragmentation of *Dalhousia* into isolated, non-interbreeding species with very restricted ranges.

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APPENDICES

APPENDIX 1. Locality data for samples used for genetic analysis.

A general description of the springs and the nature of the habitat, as well as their hydrogeology, can be found in Zeidler and Ponder (1989). Most springs, including their outflows, are densely vegetated with *Phragmites* and *Melaleuca* being the most conspicuous vegetation. Many form mounds at the head of the spring, some several metres high. In all there are approximately 60 active springs in the Dalhousie Springs complex.

Abbreviations: Coll. – collectors:– DC – D. Colgan, DM – D. MacIntosh, JW – Janet Waterhouse, SC – Stephanie Clark, TT – T. Terzis, WP – W. Ponder. cond. – conductivity in mS cm^{-1}; Stn – field station; temp. – water temperature. The species found are indicated in square brackets:– f – *F. centralia*, g – *D. globosa*, h – *D. harrisi*.

A1, Stn. D04A, 26°23'10"S 135°32'05"E, medium spring, 30–40 m downstream from pool, pH 7.68, cond. 1.19, temp. 36°C, 4/5/1990, Coll. JW SC.[g,h]

A2, Stn. D09, 26°23'12"S 135°32'02"E, large spring, in large pool at head, on mud in deeper water (large); on edges (small), pH 7.52, cond. 1.20, temp. 36°C, 4/5/1990, Coll. WP DC TT.[g,h]

A3, Stn. D02A, 26°23'28"S 135°32'07"E, large spring, uppermost outflow, pH 7.37, cond. 1.19, temp. 41°C, 4/5/1990, Coll. JW SC DM. [h]

A3, Stn. D02B, 26°23'12"S 135°32'07"E, head of spring (not a pool), pH 7.37, cond. 1.19, temp. 41°C, 4/5/1990, Coll. JW SC DM. [g]

A6, Stn. D10, 26°23'22"S 135°31'58"E, seep, pH 7.73, cond. 1.88, temp. 27.5°C, 4/5/1990, Coll. WP. [h]

A8, Stn. D11, 26°22'58"S 135°32'07"E, small active spring, pH 7.25, cond. 1.15, temp. 38°C, 4/5/1990, Coll. DC TT. [g,h]

B1, Stn. D73, 26°24'53"S 135°31'35"E, large spring, upper outflow, root mats at edges of water where water is cooler, pH 7.56, cond. 1.13, temp. 41°C, 9/5/1990, Coll. DC SC. [g,h]

B2, Stn. D74, 26°24'48"S 135°31'36"E, medium spring, upper outflow, pH 7.63, cond. 1.21, temp. 33°C, 9/5/1990, Coll. DC SC. [h]

Ca1a, Stn. D24, hot spring flowing into head of spring Ca1, 26°24'29"S 135°31'07"E, on edges, pH 7.63, cond. 1.54, temp. 42°C, 7/5/1990, Coll. SC TT. [g]

Ca1, Stn. D25, 26°24'30"S 135°31'07"E, very large spring, main pool, small species on edge of water, large species at edge and deeper, pH 7.51, cond. 1.55, temp. 40°C, 7/5/1990, Coll. SC TT. [g,h]

Ca1, Stn. D26, 26°24'30"S 135°31'08"E, uppermost outflow, pH 7.84, cond. 1.70, temp. 38°C, 7/5/1990, Coll. SC TT. [g]

Ca1, Stn. D27, 26°24'14"S 135°31'17"E, outflow 900m from pool, pH 7.40, cond. 1.71, temp. 36°C, 7/5/1990, Coll. SC TT. [g]

Ca1, Stn. D28, 26°24'16"S 135°31'14"E, outflow 600m from pool, pH 7.86, cond. 1.78, temp. 37°C, 7/5/1990, Coll. SC TT. [g]

Ca1, Stn. D46, outflow 200m from pool, 26°24'25"S 135°31'10"E, all over, pH 7.65, cond. 1.65, temp. 38°C, 7/5/1990, Coll. SC TT. [g]

Ca2, Stn. D78, 26°24'26"S 135°30'58"E, medium spring flowing into Ca1, upper outflow, pH 7.65, cond. 1.81, temp. 42°C, 10/5/1990, Coll. JW. [h]

Ca3, Stn. D76, 26°24'21"S 135°30'51"E, small active spring, at spring head, pH 7.20, cond. 1.51, temp. 29°C, 10/5/1990, Coll. JW DM. [h]

Ca5, Stn. D75, "Duck Pond", 26°24'19"S 135°30'43"E, large circular pool, pH 7.62, cond. 1.25, temp. 34°C, 10/5/1990, Coll. JW DM. [h]

Ca7, Stn. D34, 26°24'40"S 135°30'50"E, small trickle at spring head, pH 6.24, cond. 8.52, temp. 26°C, 7/5/1990, Coll. WP. [h]

Ca7, Stn. D35, 26°24'26"S 135°31'01"E, medium spring, upper outflow, pH 7.73, cond. 2.67, temp. 27°C, 7/5/1990, Coll. WP. [h]

Ca8, Stn. D38, a very small seep very near spring Ca8 and about 60 m W of western end of Ca1 pool, 26°24'27"S 135°31'00"E, on mud, pH 7.38, cond. 4.88, temp. 26°C, 7/5/1990, Coll. WP DM. [h]

Ca8, Stn. D77, 26°24'25"S 135°31'02"E, small pool at head of medium spring, pH 7.66, cond. 1.50, temp. 43°C, 10/5/1990, Coll. JW. [g,h]

Ca9, Stn. D64, 26°24'06"S 135°31'14"E, outflow of medium spring, pH 7.20, cond. 1.20, temp. 38.5°C, 8/5/1990, Coll. SC TT. [g]

Ca11, Stn. D33, 26°24'34"S 135°30'49"E, seepage in channel, pH 7.69, cond. 2.60, temp. 23°C, 6/5/1990, Coll. WP. [h]

Ca12, Stn. D36, 26°24'36"S 135°30'44"E, seepage on mound, pH 7.27, cond. 2.10, temp. 34.5°C, 7/5/1990, Coll. WP. [h]

Cb2, Stn. D51, 26°25'25"S 135°30'27"E, main pool of large spring, pH 7.35, cond. 1.81, temp. 36°C, 8/5/1990, Coll. JW DM. [g]

Cb2, Stn. D52, 26°25'22"S 135°30'28"E, small pond above main pool, pH 7.09, cond. 2.35, temp. 40.5°C, 8/5/1990, Coll. JW. [g]

Cb4, Stn. D81, 26°25'44"S 135°31'15"E, small, active spring, spring head, pH 7.40, cond. 0.98, temp. 37°C, 10/5/1990, Coll. WP TT. [h]

Cb5, Stn. D48, 26°25'56"S 135°30'12"E, small trickle, at head, pH 7.04, cond. 3.50, temp. 20°C, 8/5/1990, Coll. JW. [h]

Cb5, Stn. D49, 26°25'55"S 135°30'13"E, upper middle outflow, small spring, pH 7.30, cond. 2.59, temp. 21°C, 8/5/1990, Coll. JW. [h]

Cc1, Stn. D59, 26°25'13"S 135°29'33"E, pool at head of large spring, pH 7.45, cond. 2.47, temp. 38.5°C, 8/5/1990, Coll. WP DC. [g,h]

Cc3, Stn. D61, 26°25'47"S 135°29'24"E, pool at head of very large spring, small species on edge, large species down to 2m+, pH 7.45, cond. 1.68, temp. 39°C, 9/5/1990, Coll. WP TT. [g,h]

Cc4, Stn. D57, 26°24'10"S 135°29'20"E, large spring, in upper outflow, pH 7.60, cond. 1.45, temp. 38°C, 8/5/1990, Coll. WP, DC. [h]

Cc8, Stn. D69, 26°25'48"S 135°29'54"E, small trickle on large mound, upper outflow, pH 7.30, cond. 2.72, temp. 24°C, 9/5/1990, Coll. DC SC. [h]

Cd1, Stn. D40, 26°25'00"S 135°30'19"E, large spring, in below head, small species on edge, large species throughout pool, pH 7.12, cond. 1.55, temp. 36°C, 7/5/1990, Coll. WP DM. [h,g]

Cd1, Stn. D41, 26°24'58"S 135°30'20"E, head of spring, in outflow of small hot spring flowing into main pool, pH 7.75, cond. 1.39, temp. 39.5°C, 7/5/1990, Coll. WP. [g]

Cd1, Stn. D42, 26°24'58"S 135°30'21"E, upper ouflow 100m down from pool, pH 7.67, cond. 1.45, temp. 35°C, 7/5/1990, Coll. WP. [g]

Cd1, Stn. D43, 26°24'57"S 135°30'21"E, middle outflow, 250m from pool, pH 7.79, cond. 1.46, temp. 34.5°C, 7/5/1990, Coll. WP. [g]

Cd2, Stn. D80, 26°24'12"S 135°30'12"E, very large spring, pool at head, pH 7.89, cond. 1.31, temp. 33°C, 10/5/1990, Coll. WP TT. [g,h]

Cd3, Stn. D79, 26°24'19"S 135°30'06"E, small seep, at head, pH 7.32, cond. 1.45, temp. 34°C, 10/5/1990, Coll. WP TT. [h]

Cd5, Stn. D63, 26°24'38"S 135°30'06"E, small spring, at head, pH 7.24, cond. 1.35, temp. 39°C, 10/5/1990, Coll. WP TT. [h]

Cd8, Stn. D72, 26°24'50"S 135°30'24"E, large spring, upper outflow, pH 7.70, cond. 1.30, temp. 40°C, 9/5/1990, Coll. DC SC. [g]

Cd9, Stn. D71, 26°24'48"S 135°30'24"E, seepage on large mound, pH 7.63, cond. 1.51, temp. 20°C, 9/5/1990, Coll. DC SC. [h]

Cd11, Stn. D70, 26°24'40"S 135°30'29"E, small seepage on large mound, temp. 24°C, 9/5/1990, Coll. DC SC. [f]

Da1, Stn. D56, 26°26'58"S 135°29'08"E, small seepage on large mound, pH 6.99, cond. 2.96, temp. 24°C, 8/5/1990, Coll. WP TT. [h]

Da2, Stn. D45, 26°26'34"S 135°29'25"E, medium spring, small pool in upper outflow, pH 7.38, cond. 1.57, temp. 32°C, 8/5/1990, Coll. JW DM. [h]

Da3, Stn. D44, 26°26'34"S 135°29'33"E, medium spring, upper outflow, pH 6.51, cond. 1.57, temp. 34.5°C, 8/5/1990, Coll. JW DM. [h]

Db1, Stn. D31, 26°26'56"S 135°30'02"E, small seepage on large mound, temp. 24.5°C, 6/5/1990, Coll. WP DC. [h]

Db2, Stn. D20, 26°27'15"S 135°30'12"E, large spring, near head, pH 6.66, cond. 2.06, temp. 31°C, 6/5/1990, Coll. WP DC. [h]

Db4, Stn. D29A, 26°27'22"S 135°30'24"E, cold seep on large mound, pH 6.96, cond. 1.91, temp. 28°C, 6/5/1990, Coll. WP DC. [h]

E1, Stn. D06, 26°29'52"S 135°30'09"E, medium spring, upper outflow, pH 7.82, cond. 1.60, temp. 30°C, 5/5/1990, Coll. JW SC. [h]

E1, Stn. D62, 26°29'51"S 135°30'09"E, lower swampy ouflow, pH 7.81, cond. 1.75, temp. 16.5°C, 9/5/1990, Coll. WP TT. [f]

E2, Stn. D07, 26°30'06"S 135°30'04"E, small spring, at head, pH 7.80, cond. 1.86, temp. 31°C, 5/5/1990, Coll. JW SC. [h]

E3, Stn. D23A, 26°28'08"S 135°29'42"E, small trickle, spring head, pH 7.11, cond. 5.46, temp. 22°C, 6/5/1990, Coll. JW DM. [f]

E3, Stn. D23B, 26°28'04"S 135°29'41"E, about 20m from D23A, in open boggy area, pH 7.11, cond. 5.46, temp. 19°C, 6/5/1990, Coll. JW DM. [f]

E5, Stn. D08, 26°29'08"S 135°29'38"E, small active spring, pH 7.18, cond. 1.80, temp. 25°C, 6/5/1990, Coll. JW DM. [h]

E7, Stn. D17A, 26°29'47"S 135°30'00"E, small warm seep on large mound, pH 7.5, cond. 2.7, temp. 31°C, 5/5/1990, Coll. WP DC. [h]

E8, Stn. D18, 26°29'47"S 135°29'55"E, small seep on large mound, on wet mud, temp. 25°C, 5/5/1990, Coll. WP DC. [h]

F1, Stn. D54, 26°30'54"S 135°29'11"E, small active spring on large mound, at head, pH 7.20, cond. 1.81, temp. 21°C, 8/5/1990, Coll. WP. [h]

F2, Stn. D55, 26°30'37"S 135°29'24"E, small active spring, upper outflow, pH 7.07, cond. 1.18, temp. 28°C, 8/5/1990, Coll. WP. [h]

F9, Stn. D53, 26°31'06"S 135°29'15"E, small seep, pH 6.45, cond. 1.91, temp. 20°C, 8/5/1990, Coll. WP DC. [f]

Ga1, Stn. D13, 26°31'36"S 135°29'59"E, small seep, pH 7.5, cond. 2.39, temp. 16°C, 5/5/1990, Coll. DC TT. [f]

Ga2, Stn. D05A, 26°31'39"S 135°29'58"E, medium spring, in pool at head, pH 6.80, cond. 1.96, temp. 31°C, 5/5/1990, Coll. JW SC. [h]

Ga2, Stn. D05B, 26°31'42"S 135°29'59"E, middle outflow, pH 7.30, cond. 2.06, temp. 20°C, 5/5/1990, Coll. JW SC. [f]

Ga3, Stn. D14, 26°31'27"S 135°30'00"E, medium spring, pool at head, pH 7.33, cond. 2.57, temp. 34°C, 5/5/1990, Coll. WP DC TT. [h]

Ga4, Stn. D12, 26°31'35"S 135°29'59"E, small seep on large mound, temp. 20°C, 5/5/1990, Coll. DC TT. [h]

Ga6, Stn. D15, 26°31'05"S 135°30'01"E, small seepage on medium mound, pH 7.35, cond. 6.26, temp. 21°C, 5/5/1990, Coll. WP DC. [f]

Ga6, Stn. D16, 26°31'06"S 135°30'03"E, small trickle, pH 7.48, cond. 2.19, temp. 35.5°C, 5/5/1990, Coll. WP DC. [h]

H1, Stn. D01, 26°33'43"S 135°28'47"E, small active spring, medium mound, pH 7.24, cond. 2.02, temp. 24°C, 4/5/1990, Coll. WP DC JW SC. [h]

H3, Stn. D19, Emily Springs, 26°33'23"S 135°27'15"E, large spring, upper outflow, pH 6.71, cond. 1.89, temp. 22°C, 6/5/1990, Coll. WP DC. [h]

APPENDIX 2

Measurement tables for shells

Table 2. Means and standard deviations (below) of shell measurements and ratios for *Dalhousia globosa* and *D. harrisi*.

Dalhousia globosa

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring A1 (D4A), Female, N=58										
	3.40	2.62	1.87	1.66	2.86	0.77	0.89	0.55	0.85	0.63
	0.55	0.39	0.29	0.23	0.43	0.04	0.05	0.03	0.03	0.02
	Male, N=35									
	3.34	2.54	1.79	1.60	2.78	0.76	0.90	0.54	0.83	0.63
	0.45	0.30	0.22	0.18	0.35	0.04	0.04	0.03	0.05	0.02
Spring A2 (D9), Female, N=28										
	4.27	3.17	2.25	1.98	3.53	0.74	0.88	0.53	0.83	0.63
	0.19	0.13	0.10	0.09	0.15	0.03	0.03	0.02	0.02	0.02
	Male, N=27									
	4.08	3.06	2.17	1.88	3.37	0.75	0.87	0.53	0.83	0.61
	0.30	0.22	0.16	0.13	0.22	0.04	0.05	0.02	0.01	0.02
Spring A3 (D2B), Female, N=27										
	2.51	1.74	1.27	1.17	2.04	0.70	0.92	0.51	0.81	0.67
	0.24	0.17	0.13	0.11	0.19	0.03	0.04	0.03	0.02	0.02
	Male, N=25									
	2.48	1.72	1.23	1.16	2.00	0.69	0.94	0.50	0.81	0.68
	0.22	0.15	0.10	0.09	0.17	0.03	0.03	0.02	0.02	0.02
Spring Ca1 (D25, D26, D28, D46), Female, N=119										
	2.81	2.21	1.55	1.42	2.40	0.79	0.91	0.56	0.86	0.64
	0.72	0.56	0.40	0.37	0.58	0.05	0.05	0.05	0.03	0.03
	Male, N=81									
	2.70	2.12	1.47	1.36	2.32	0.79	0.93	0.54	0.86	0.64
	0.64	0.50	0.36	0.33	0.51	0.03	0.04	0.03	0.02	0.03
Spring Ca1a (D24), Female, N=5										
	2.83	1.98	1.44	1.25	2.29	0.70	0.87	0.51	0.81	0.63
	0.21	0.17	0.14	0.12	0.20	0.02	0.04	0.02	0.03	0.02
	Male, N=6									
	2.79	1.88	1.38	1.26	2.25	0.68	0.91	0.50	0.81	0.67
	0.38	0.24	0.18	0.14	0.30	0.03	0.03	0.02	0.02	0.02
Spring Ca9 (D64), Female, N=16										
	2.77	1.86	1.30	1.25	2.21	0.67	0.96	0.47	0.79	0.67
	0.29	0.22	0.15	0.14	0.24	0.04	0.03	0.02	0.02	0.03
	Male, N=34									
	2.58	1.73	1.22	1.17	2.06	0.67	0.96	0.47	0.80	0.68
	0.29	0.17	0.14	0.11	0.20	0.04	0.05	0.02	0.02	0.03
Spring Cb2 (D51, D52), Female, N=52										
	2.90	2.11	1.50	1.34	2.42	0.73	0.90	0.52	0.83	0.64
	0.46	0.37	0.27	0.20	0.41	0.04	0.05	0.03	0.03	0.03
	Male, N=57									
	2.86	2.11	1.51	1.34	2.41	0.74	0.90	0.53	0.84	0.64
	0.48	0.43	0.30	0.22	0.45	0.05	0.05	0.04	0.04	0.04
Spring Cc3 (D61), Female, N=30										
	3.23	2.48	1.72	1.53	2.69	0.77	0.89	0.53	0.83	0.62
	0.29	0.22	0.17	0.13	0.22	0.04	0.05	0.03	0.02	0.02
	Male, N=25									
	3.08	2.34	1.61	1.47	2.56	0.76	0.91	0.52	0.83	0.63
	0.22	0.18	0.12	0.10	0.18	0.03	0.04	0.03	0.02	0.03
Spring Cd1 (D40–D43), Female, N=143										
	3.24	2.47	1.74	1.54	2.70	0.77	0.89	0.54	0.84	0.63
	0.70	0.48	0.32	0.28	0.55	0.05	0.04	0.04	0.03	0.02
	Male, N=69									
	3.29	2.48	1.74	1.56	2.72	0.76	0.90	0.53	0.83	0.63
	0.69	0.47	0.34	0.28	0.52	0.04	0.05	0.03	0.03	0.03

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Dalhousia harrisi										
Spring A2 (D9), Female, N=49										
	2.88	1.88	1.35	1.29	2.30	0.65	0.96	0.47	0.80	0.69
	0.26	0.17	0.14	0.10	0.20	0.03	0.06	0.02	0.02	0.03
	Male, N=54									
	2.65	1.73	1.24	1.19	2.11	0.65	0.96	0.47	0.80	0.69
	0.30	0.20	0.15	0.13	0.23	0.03	0.04	0.02	0.02	0.03
Spring A3 (D2A), Female, N=28										
	2.80	1.79	1.27	1.25	2.17	0.64	0.98	0.46	0.78	0.70
	0.23	0.15	0.11	0.11	0.14	0.03	0.05	0.02	0.02	0.03
	Male, N=27									
	2.69	1.70	1.21	1.20	2.06	0.63	0.99	0.45	0.77	0.70
	0.15	0.10	0.06	0.08	0.10	0.03	0.05	0.02	0.02	0.03
Spring A6 (D10), Female, N=12										
	2.95	1.87	1.36	1.25	2.27	0.64	0.92	0.46	0.77	0.67
	0.18	0.15	0.14	0.11	0.14	0.02	0.05	0.03	0.02	0.03
	Male, N=13									
	2.80	1.83	1.33	1.22	2.17	0.65	0.92	0.46	0.78	0.67
	0.15	0.07	0.07	0.06	0.09	0.03	0.04	0.02	0.02	0.02
Spring B2 (D74), Female, N=19										
	2.90	1.86	1.34	1.27	2.26	0.64	0.96	0.46	0.78	0.69
	0.49	0.31	0.24	0.20	0.35	0.03	0.05	0.02	0.02	0.04
	Male, N=36									
	2.74	1.75	1.26	1.18	2.13	0.64	0.94	0.46	0.78	0.68
	0.55	0.29	0.23	0.16	0.36	0.04	0.06	0.02	0.03	0.04
Spring Ca1 (D25), Female, N=22										
	2.80	2.01	1.44	1.35	2.29	0.72	0.94	0.51	0.82	0.67
	0.23	0.15	0.11	0.10	0.17	0.04	0.04	0.02	0.02	0.04
	Male, N=28									
	2.79	1.96	1.42	1.33	2.27	0.70	0.93	0.51	0.81	0.68
	0.28	0.16	0.13	0.11	0.20	0.03	0.04	0.02	0.02	0.03
Spring Ca2 (D78), Female, N=22										
	2.44	1.55	1.13	1.12	1.90	0.64	0.99	0.46	0.78	0.72
	0.25	0.14	0.12	0.13	0.16	0.03	0.05	0.03	0.03	0.03
	Male, N=28									
	2.30	1.45	1.06	1.05	1.80	0.63	0.99	0.46	0.78	0.73
	0.22	0.12	0.10	0.11	0.14	0.02	0.04	0.02	0.03	0.04
Spring Ca3 (D76), Female, N=24										
	3.77	2.39	1.71	1.56	2.88	0.64	0.92	0.45	0.77	0.66
	0.69	0.42	0.30	0.25	0.46	0.04	0.05	0.03	0.02	0.03
	Male, N=26									
	3.09	1.98	1.41	1.31	2.39	0.65	0.94	0.46	0.78	0.67
	0.59	0.31	0.24	0.18	0.38	0.04	0.04	0.02	0.03	0.03
Spring Ca5 (D75), Female, N=27										
	4.13	2.97	2.05	1.86	3.27	0.72	0.91	0.50	0.79	0.63
	0.53	0.41	0.27	0.21	0.38	0.03	0.05	0.02	0.02	0.03
	Male, N=23									
	3.74	2.64	1.80	1.67	2.92	0.71	0.93	0.48	0.78	0.64
	0.53	0.41	0.25	0.22	0.37	0.03	0.03	0.02	0.02	0.03
Spring Ca7 (D34, D35), Female, N=42										
	3.57	2.19	1.58	1.49	2.69	0.62	0.95	0.45	0.76	0.68
	0.84	0.45	0.33	0.29	0.54	0.03	0.04	0.02	0.04	0.03
	Male, N=58									
	3.31	2.06	1.47	1.40	2.52	0.63	0.96	0.45	0.77	0.69
	0.88	0.48	0.35	0.31	0.57	0.04	0.04	0.03	0.04	0.03
Spring Ca8 (D38, D77), Female, N=38										
	2.71	1.73	1.23	1.22	2.10	0.64	0.99	0.46	0.78	0.70
	0.38	0.20	0.18	0.17	0.26	0.04	0.07	0.03	0.04	0.04

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
	Male, N=38									
	2.48	1.64	1.14	1.14	1.95	0.66	1.00	0.46	0.79	0.69
	0.35	0.20	0.17	0.16	0.24	0.03	0.08	0.03	0.03	0.04
Spring Ca12 (D36), Female, N=25										
	2.77	1.74	1.29	1.23	2.17	0.63	0.95	0.47	0.78	0.70
	0.26	0.14	0.10	0.11	0.19	0.03	0.05	0.03	0.02	0.03
	Male, N=25									
	2.48	1.59	1.17	1.13	1.96	0.64	0.97	0.47	0.79	0.71
	0.28	0.14	0.13	0.12	0.20	0.03	0.04	0.02	0.02	0.03
Spring Cb4 (D81), Female, N=34										
	2.62	1.69	1.20	1.16	2.05	0.65	0.97	0.46	0.79	0.69
	0.20	0.12	0.10	0.07	0.13	0.02	0.05	0.01	0.02	0.02
	Male, N=21									
	2.37	1.56	1.10	1.07	1.87	0.66	0.98	0.47	0.79	0.69
	0.24	0.14	0.11	0.08	0.14	0.03	0.04	0.02	0.03	0.03
Spring Cb5 (D48, D49), Female, N=41										
	2.99	1.89	1.35	1.32	2.30	0.63	0.98	0.45	0.77	0.70
	0.37	0.22	0.16	0.14	0.24	0.02	0.05	0.02	0.03	0.03
	Male, N=64									
	2.70	1.72	1.24	1.22	2.11	0.64	0.99	0.46	0.78	0.71
	0.23	0.15	0.11	0.09	0.16	0.03	0.04	0.02	0.02	0.03
Spring Cc1 (D59), Female, N=24										
	2.57	1.67	1.22	1.16	2.05	0.65	0.95	0.48	0.80	0.70
	0.22	0.13	0.11	0.08	0.17	0.03	0.04	0.02	0.02	0.03
	Male, N=31									
	2.40	1.54	1.13	1.07	1.91	0.65	0.95	0.47	0.80	0.70
	0.32	0.16	0.12	0.12	0.21	0.05	0.04	0.03	0.03	0.03
Spring Cc3 (D61), Female, N=30										
	2.69	1.86	1.37	1.24	2.22	0.69	0.91	0.51	0.82	0.67
	0.26	0.15	0.13	0.09	0.19	0.03	0.04	0.02	0.02	0.03
	Male, N=25									
	2.62	1.83	1.34	1.23	2.15	0.70	0.92	0.51	0.82	0.67
	0.26	0.19	0.14	0.12	0.19	0.02	0.03	0.02	0.02	0.02
Spring Cc8 (D69), Female, N=31										
	2.91	1.82	1.31	1.28	2.23	0.63	0.98	0.45	0.77	0.70
	0.33	0.20	0.12	0.13	0.21	0.03	0.03	0.02	0.03	0.03
	Male, N=24									
	2.86	1.78	1.28	1.26	2.20	0.62	0.99	0.45	0.77	0.71
	0.21	0.10	0.10	0.07	0.15	0.02	0.05	0.02	0.02	0.02
Spring Cd1 (D40), Female, N=21										
	2.60	1.81	1.32	1.22	2.13	0.70	0.92	0.51	0.82	0.67
	0.19	0.13	0.10	0.09	0.15	0.04	0.04	0.02	0.02	0.02
	Male, N=34									
	2.54	1.84	1.28	1.20	2.07	0.73	0.94	0.50	0.82	0.67
	0.22	0.34	0.11	0.10	0.17	0.13	0.03	0.02	0.02	0.07
Spring Cd2 (D80), Female, N=24										
	2.74	1.97	1.39	1.28	2.25	0.72	0.92	0.51	0.82	0.65
	0.18	0.10	0.08	0.06	0.13	0.04	0.03	0.02	0.03	0.02
	Male, N=31									
	2.72	1.88	1.34	1.25	2.19	0.69	0.93	0.49	0.80	0.67
	0.22	0.15	0.10	0.09	0.16	0.03	0.03	0.02	0.02	0.02
Spring Cd3 (D79), Female, N=20										
	2.87	1.82	1.29	1.23	2.16	0.64	0.95	0.46	0.77	0.68
	0.51	0.21	0.15	0.12	0.23	0.08	0.04	0.06	0.09	0.03
	Male, N=24									
	2.40	1.60	1.16	1.07	1.90	0.67	0.92	0.48	0.79	0.67
	0.26	0.17	0.13	0.11	0.18	0.03	0.05	0.02	0.03	0.03

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring Cd5 (D63), Female, N=40										
	2.79	1.79	1.28	1.22	2.16	0.64	0.96	0.46	0.78	0.68
	0.32	0.15	0.14	0.13	0.21	0.04	0.05	0.02	0.02	0.03
	Male, N=65									
	2.58	1.67	1.20	1.15	2.02	0.65	0.96	0.47	0.79	0.69
	0.27	0.15	0.11	0.11	0.17	0.03	0.04	0.02	0.03	0.03
Spring Cd9 (D71), Female, N=28										
	3.54	2.17	1.52	1.42	2.61	0.61	0.93	0.43	0.74	0.65
	0.29	0.15	0.11	0.10	0.18	0.03	0.05	0.02	0.02	0.03
	Male, N=27									
	3.44	2.07	1.50	1.37	2.55	0.60	0.91	0.44	0.74	0.66
	0.27	0.17	0.11	0.11	0.18	0.03	0.06	0.02	0.02	0.03
Spring Da2 (D5), Female, N=57										
	3.02	2.01	1.45	1.37	2.35	0.67	0.94	0.48	0.78	0.68
	0.32	0.18	0.15	0.12	0.23	0.03	0.05	0.02	0.02	0.03
	Male, N=48									
	2.97	1.97	1.42	1.35	2.32	0.66	0.96	0.48	0.78	0.69
	0.32	0.21	0.17	0.13	0.23	0.02	0.05	0.02	0.02	0.03
Spring Da3a (D44), Female, N=22										
	3.00	1.94	1.41	1.30	2.30	0.65	0.92	0.47	0.77	0.67
	0.26	0.15	0.12	0.08	0.19	0.03	0.04	0.02	0.02	0.02
	Male, N=33									
	2.95	1.89	1.40	1.29	2.28	0.64	0.92	0.48	0.77	0.68
	0.31	0.21	0.16	0.12	0.23	0.03	0.04	0.02	0.02	0.03
Spring Db1 (D31), Female, N=14										
	2.78	1.80	1.31	1.22	2.18	0.65	0.94	0.47	0.79	0.68
	0.28	0.16	0.14	0.11	0.19	0.03	0.05	0.02	0.02	0.02
	Male, N=33									
	2.58	1.68	1.23	1.15	2.04	0.65	0.94	0.48	0.79	0.69
	0.27	0.16	0.13	0.10	0.19	0.02	0.05	0.02	0.02	0.03
Spring Db4a (D21, D29), Female, N=27										
	2.59	1.64	1.19	1.14	2.03	0.64	0.97	0.46	0.79	0.70
	0.31	0.16	0.13	0.13	0.22	0.03	0.04	0.02	0.02	0.03
	Male, N=14									
	1.48	1.09	1.06	1.86	1.57	0.74	1.76	0.71	1.06	1.71
	0.10	0.07	0.08	0.09	0.51	0.02	0.07	0.03	0.35	0.06
Spring E1 (D6), Female, N=24										
	3.60	2.29	1.63	1.54	2.77	0.64	0.95	0.45	0.77	0.67
	0.34	0.23	0.17	0.13	0.25	0.03	0.05	0.02	0.02	0.03
	Male, N=26									
	3.41	2.17	1.52	1.47	2.59	0.64	0.97	0.45	0.76	0.68
	0.44	0.29	0.22	0.16	0.32	0.03	0.05	0.02	0.02	0.03
Spring E2 (D7), Female, N=26										
	3.04	1.99	1.44	1.36	2.36	0.66	0.94	0.47	0.78	0.68
	0.31	0.21	0.16	0.12	0.23	0.03	0.05	0.02	0.02	0.03
	Male, N=29									
	2.89	1.89	1.37	1.29	2.25	0.65	0.94	0.47	0.78	0.68
	0.26	0.17	0.14	0.12	0.21	0.02	0.04	0.02	0.02	0.03
Spring E5 (D8), Female, N=13										
	3.03	2.06	1.47	1.35	2.36	0.68	0.93	0.48	0.78	0.66
	0.49	0.29	0.26	0.14	0.36	0.03	0.07	0.02	0.02	0.03
	Male, N=9									
	2.54	1.74	1.23	1.23	2.01	0.69	1.00	0.49	0.79	0.71
	0.33	0.20	0.14	0.21	0.23	0.02	0.14	0.02	0.02	0.10

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring E7a (D17A), Female, N=32										
	2.86	1.72	1.26	1.22	2.14	0.60	0.97	0.44	0.75	0.71
	0.27	0.12	0.10	0.09	0.17	0.03	0.04	0.02	0.02	0.02
	Male, N=18									
	2.61	1.62	1.18	1.15	2.00	0.62	0.98	0.45	0.77	0.71
	0.18	0.10	0.07	0.10	0.11	0.03	0.05	0.02	0.02	0.04
Spring E8 (D18), Female, N=25										
	2.91	1.74	1.27	1.26	2.19	0.60	1.00	0.44	0.75	0.73
	0.28	0.15	0.12	0.10	0.19	0.02	0.03	0.01	0.02	0.03
	Male, N=25									
	2.84	1.73	1.24	1.21	2.15	0.61	0.98	0.44	0.76	0.70
	0.24	0.13	0.11	0.09	0.17	0.02	0.05	0.02	0.01	0.02
Spring F1 (D54), Female, N=46										
	3.44	2.18	1.57	1.43	2.62	0.63	0.91	0.46	0.76	0.66
	0.39	0.23	0.19	0.16	0.28	0.02	0.05	0.02	0.02	0.04
	Male, N=58									
	3.34	2.07	1.51	1.37	2.51	0.62	0.91	0.45	0.75	0.66
	0.44	0.26	0.20	0.16	0.31	0.03	0.06	0.02	0.02	0.04
Spring Ga2 (D5), Female, N=27										
	2.51	1.61	1.16	1.07	1.99	0.64	0.92	0.47	0.80	0.67
	0.35	0.17	0.15	0.15	0.23	0.05	0.07	0.06	0.07	0.05
	Male, N=23									
	2.27	1.48	1.04	0.98	1.79	0.65	0.96	0.46	0.79	0.67
	0.30	0.18	0.15	0.11	0.22	0.03	0.09	0.04	0.04	0.04
Spring Ga3a (D14), Female, N=22										
	3.10	1.93	1.38	1.32	2.31	0.62	0.96	0.44	0.74	0.69
	0.28	0.19	0.13	0.12	0.19	0.02	0.035	0.02	0.03	0.02
	Male, N=28									
	2.90	1.82	1.29	1.26	2.19	0.63	0.97	0.45	0.76	0.69
	0.30	0.19	0.16	0.15	0.23	0.03	0.06	0.02	0.03	0.03
Spring Ga6b (D16), Female, N=50										
	3.07	1.97	1.47	1.29	2.41	0.64	0.88	0.48	0.79	0.66
	0.57	0.31	0.25	0.18	0.39	0.04	0.05	0.02	0.03	0.03
	Male, N=52									
	2.64	1.73	1.30	1.16	2.12	0.66	0.90	0.49	0.81	0.67
	0.54	0.32	0.25	0.18	0.37	0.04	0.05	0.02	0.03	0.03
Spring H1 (D1), Female, N=28										
	3.13	1.99	1.41	1.34	2.40	0.64	0.95	0.45	0.77	0.68
	0.34	0.19	0.14	0.12	0.22	0.03	0.05	0.02	0.02	0.02
	Male, N=27									
	2.88	1.90	1.30	1.27	2.22	0.66	0.976	0.45	0.77	0.67
	0.19	0.12	0.09	0.09	0.14	0.02	0.04	0.02	0.02	0.02
Spring H3 (D19), Female, N=13										
	3.35	2.10	1.51	1.42	2.55	0.63	0.94	0.45	0.76	0.68
	0.18	0.14	0.12	0.08	0.15	0.02	0.04	0.02	0.02	0.02
	Male, N=12									
	3.35	2.03	1.46	1.40	2.51	0.61	0.96	0.44	0.75	0.69
	0.21	0.11	0.06	0.04	0.09	0.03	0.04	0.02	0.03	0.02

Table 3. Means and standard deviations (below) of shell measurements and ratios for *Fluvidona centralia*.

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring Cd11 (D70), Female, N = 6										
	1.91	1.16	0.78	0.69	1.39	0.61	0.90	0.41	0.73	0.60
	0.16	0.07	0.08	0.05	0.13	0.03	0.03	0.02	0.03	0.02
Male, N=14										
	1.71	1.05	0.70	0.63	1.26	0.62	0.90	0.41	0.74	0.60
	0.11	0.07	0.06	0.06	0.09	0.03	0.06	0.02	0.02	0.03
Spring E1 (D62), Female, N=16										
	2.63	1.56	1.06	0.91	1.89	0.60	0.86	0.41	0.72	0.58
	0.22	0.12	0.09	0.07	0.15	0.03	0.05	0.03	0.03	0.03
Male, N=4										
	2.42	1.43	1.01	0.83	1.76	0.59	0.83	0.42	0.73	0.58
	0.12	0.07	0.07	0.01	0.08	0.02	0.05	0.03	0.03	0.03
Spring E3 (D23A), Female, N=18										
	2.45	1.54	1.05	0.88	1.80	0.63	0.84	0.43	0.74	0.57
	0.17	0.09	0.07	0.05	0.10	0.02	0.04	0.02	0.02	0.02
Male, N=2										
	2.22	1.35	0.92	0.78	1.58	0.61	0.85	0.41	0.71	0.57
	0.23	0.10	0.09	0.06	0.17	0.02	0.02	0.00	0.00	0.01
Spring F9 (D53), Female, N=14										
	2.20	1.36	0.92	0.80	1.59	0.62	0.87	0.42	0.72	0.59
	0.22	0.10	0.09	0.06	0.14	0.03	0.05	0.02	0.03	0.01
Male, N=5										
	2.26	1.33	0.90	0.76	1.60	0.59	0.85	0.40	0.71	0.58
	0.29	0.15	0.09	0.09	0.18	0.02	0.03	0.02	0.03	0.01
Spring Ga1 (D13), Female, N=10										
	2.11	1.37	0.93	0.81	1.61	0.65	0.87	0.44	0.76	0.59
	0.18	0.09	0.09	0.06	0.15	0.03	0.04	0.03	0.02	0.02
Male, N=10										
	1.86	1.17	0.80	0.70	1.40	0.63	0.88	0.43	0.75	0.59
	0.23	0.15	0.11	0.09	0.18	0.03	0.04	0.02	0.02	0.02
Spring Ga2A (D5), Female, N=16										
	2.90	1.76	1.26	1.00	2.11	0.61	0.80	0.43	0.73	0.57
	0.23	0.11	0.07	0.06	0.12	0.02	0.04	0.02	0.02	0.02
Male, N=3										
	3.15	1.78	1.30	1.02	2.24	0.57	0.78	0.41	0.71	0.57
	0.26	0.07	0.14	0.07	0.20	0.03	0.03	0.02	0.03	0.03

APPENDIX 3

Allozyme data

Table 4. Measures of genetic variation within samples of *Dalhousia globosa*. The columns give the mean sample size and mean number of alleles per locus, the percentage of loci where more than one allozyme was detected, the mean observed heterozygosity and Nei's (1978) unbiased estimate of expected heterozygosity. Standard deviations are given in brackets.

Population	Mean sample size per Locus	Mean no. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity: Direct-count	Mean heterozygosity: HdyWbg expected
1. D4A (A1)	6.6 (.2)	1.3 (.1)	21.9	.057 (.022)	.075 (.031)
2. D9 (A2)	6.0 (.2)	1.2 (.1)	12.5	.067 (.035)	.063 (.031)
3. D2A (A3)	8.3 (.5)	1.4 (.1)	28.1	.077 (.036)	.106 (.037)
4. D11a (A8)	19.2 (1.8)	1.5 (.1)	37.5	.043 (.015)	.084 (.027)
5. D73 (B1)	11.5 (1.3)	1.5 (.2)	34.4	.067 (.024)	.113 (.038)
6. D24 (Ca1a, hot spr)	13.9 (1.3)	1.2 (.1)	15.6	.018 (.008)	.021 (.009)
7. D25 (Ca1 pool)	54.5 (4.0)	1.8 (.2)	53.1	.046 (.016)	.099 (.030)
8. D26 (Ca1 outflw)	35.0 (4.0)	1.4 (.1)	28.1	.029 (.014)	.057 (.025)
9. D28 (Ca1 outflw)	31.4 (3.9)	1.3 (.1)	21.9	.043 (.019)	.066 (.028)
10. D46 (Ca1 outflw)	27.0 (3.1)	1.3 (.1)	18.8	.048 (.023)	.063 (.028)
11. D77 (Ca8)	10.1 (1.7)	1.2 (.1)	9.4	.015 (.015)	.043 (.028)
12. D77 hybrids	7.8 (1.0)	1.2 (.1)	12.5	.050 (.036)	.049 (.026)
13. D64 (Ca9)	30.3 (4.0)	1.3 (.1)	21.9	.028 (.015)	.064 (.029)
14. D51 (Cb2)	13.0 (.4)	1.4 (.1)	31.3	.068 (.024)	.092 (.031)
15. D52 (Cb2)	6.3 (.3)	1.4 (.1)	21.9	.075 (.033)	.107 (.039)
16. D59 (Cc1)	5.9 (.2)	1.2 (.1)	18.8	.071 (.032)	.097 (.036)
17. D61 (Cc3)	6.8 (.5)	1.3 (.1)	18.8	.090 (.042)	.079 (.033)
18. D40 (Cd1 pool)	9.0 (.5)	1.3 (.1)	18.8	.084 (.033)	.088 (.035)
19. D43 (Cd1)	7.4 (.4)	1.5 (.2)	28.1	.119 (.039)	.138 (.043)
20. D41 (Cd1 head)	7.3 (.3)	1.3 (.1)	18.8	.079 (.034)	.089 (.035)
21. D42 (Cd1 outflw)	4.5 (.2)	1.3 (.1)	25.0	.130 (.048)	.114 (.038)
22. D80 (Cd2)	6.5 (.8)	1.3 (.1)	21.9	.052 (.026)	.082 (.032)
23. D80 hybrids	9.6 (1.1)	1.5 (.1)	37.5	.101 (.037)	.119 (.035)
24. D72 (Cd8)	5.5 (.3)	1.2 (.1)	18.8	.055 (.027)	.054 (.024)

Table 5. Measures of genetic variation within samples of *Dalhousia harrisi*. The columns give the mean sample size and mean number of alleles per locus, the percentage of loci where more than one allozyme was detected, the mean observed heterozygosity and Nei's (1978) unbiased estimate of expected heterozygosity. Standard deviations are given in brackets.

Population	Mean sample size per Locus	Mean No. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity Direct-count	Mean heterozygosity HdyWbg expected
1. D4A (A1)	18.1 (1.8)	1.3 (.1)	28.1	.064 (.025)	.083 (.030)
2. D9 (A2)	20.5 (2.1)	1.3 (.1)	28.1	.048 (.020)	.060 (.024)
3. D2 (A3)	6.4 (.4)	1.2 (.1)	15.6	.044 (.023)	.048 (.023)
4. D10 (A6)	18.1 (1.8)	1.3 (.1)	18.8	.078 (.032)	.076 (.031)
5. D11b (A8)	5.0 (.3)	1.1 (.1)	9.4	.031 (.019)	.027 (.017)
6. D73 (B1)	7.9 (.8)	1.4 (.1)	31.3	.060 (.023)	.103 (.032)
7. D74 (B2)	9.5 (.3)	1.3 (.1)	25.0	.048 (.019)	.063 (.021)
8. D25 (Ca1 pool)	17.1 (1.9)	1.5 (.2)	28.1	.039 (.017)	.063 (.026)
9. D78 (Ca2)	27.0 (3.8)	1.3 (.1)	18.8	.027 (.015)	.043 (.025)
10. D76 (Ca3)	24.8 (3.4)	1.4 (.1)	28.1	.052 (.021)	.084 (.030)
11. D75 (Ca5)	31.9 (3.2)	1.3 (.1)	25.0	.051 (.025)	.071 (.033)
12. D34 (Ca7)	25.6 (3.9)	1.1 (.1)	3.1	.002 (.002)	.002 (.002)
13. D35 (Ca7)	27.8 (3.9)	1.1 (.1)	9.4	.004 (.003)	.022 (.016)
14. D38 (Ca8)	17.6 (1.8)	1.3 (.2)	12.5	.067 (.037)	.066 (.033)
15. D77 (Ca8)	7.5 (1.1)	1.2 (.1)	15.6	.025 (.018)	.063 (.029)
16. D36 (Ca12)	27.2 (3.9)	1.3 (.1)	18.8	.039 (.024)	.046 (.022)
17. D33 (Ca11)	25.8 (3.5)	1.3 (.1)	25.0	.045 (.023)	.064 (.028)
18. D81 (Cb4)	8.4 (.6)	1.2 (.1)	21.9	.060 (.028)	.061 (.025)
19. D48 (Cb5 head)	18.9 (2.1)	1.3 (.1)	18.8	.039 (.021)	.073 (.030)
20. D49 (Cb5 outflw)	6.0 (.1)	1.2 (.1)	18.8	.059 (.030)	.079 (.032)
21. D59 (Cc1)	6.3 (.2)	1.2 (.1)	21.9	.057 (.024)	.077 (.028)
22. D61 (Cc3)	8.0 (.5)	1.2 (.1)	12.5	.030 (.015)	.036 (.018)
23. D57 (Cc4)	16.5 (1.7)	1.2 (.1)	12.5	.027 (.016)	.043 (.023)
24. D69 (Cc8)	8.7 (.4)	1.2 (.1)	15.6	.027 (.015)	.053 (.025)
25. D40 (Cd1 pool)	6.9 (.3)	1.4 (.1)	31.3	.066 (.024)	.114 (.037)

Population	Mean sample size per Locus	Mean No. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity	
				Direct-count	HdyWbg expected
26. D80B (Cd2)	18.1	1.4	31.3	.068	.084
	(2.5)	(.1)		(.024)	(.028)
27. D79 (Cd3)	5.5	1.3	21.9	.067	.098
	(.2)	(.1)		(.029)	(.036)
28. D63 (Cd5)	5.4	1.3	21.9	.052	.079
	(.1)	(.1)		(.019)	(.028)
29. D71 (Cd9)	6.4	1.1	12.5	.042	.045
	(.3)	(.1)		(.020)	(.022)
30. D56 (Da1)	5.9	1.2	21.9	.040	.076
	(.2)	(.1)		(.020)	(.029)
31. D45 (Da2)	17.9	1.2	12.5	.036	.072
	(2.0)	(.1)		(.019)	(.035)
32. D44 (Da3)	11.8	1.2	18.8	.014	.053
	(.4)	(.1)		(.008)	(.024)
33. D31 (Db1)	5.9	1.3	18.8	.026	.082
	(.1)	(.1)		(.017)	(.032)
34. D20 (Db2)	9.5	1.3	31.3	.063	.128
	(.3)	(.1)		(.024)	(.035)
35. D29 (Db4)	6.0	1.2	15.6	.020	.062
	(.2)	(.1)		(.012)	(.031)
36. D6 (E1)	20.0	1.4	34.4	.069	.095
	(1.6)	(.1)		(.024)	(.029)
37. D7 (E2)	8.8	1.5	34.4	.069	.109
	(.3)	(.1)		(.022)	(.031)
38. D8 (E5)	23.3	1.3	25.0	.031	.036
	(1.6)	(.1)		(.013)	(.015)
39. D17A (E7)	17.4	1.3	25.0	.046	.069
	(1.3)	(.1)		(.020)	(.029)
40. D18 (E8)	21.4	1.3	15.6	.042	.069
	(1.9)	(.1)		(.020)	(.033)
41. D54 (F1)	21.0	1.3	25.0	.035	.056
	(1.8)	(.1)		(.016)	(.024)
42. D55 (F2)	17.4	1.3	21.9	.043	.067
	(1.6)	(.1)		(.019)	(.029)
43. D5 (Ga2)	25.4	1.3	31.3	.043	.066
	(2.2)	(.1)		(.016)	(.024)
44. D14 (Ga3)	32.8	1.3	25.0	.058	.060
	(1.9)	(.1)		(.025)	(.026)
45. D12 (Ga4)	19.3	1.2	15.6	.059	.071
	(1.9)	(.1)		(.029)	(.033)
46. D16 (Ga6)	19.9	1.5	37.5	.047	.082
	(.5)	(.1)		(.017)	(.028)
47. D1 (H1)	19.5	1.3	18.8	.037	.069
	(1.8)	(.1)		(.021)	(.029)
48. D19 (H3)	17.6	1.3	21.9	.053	.079
	(1.6)	(.1)		(.025)	(.033)

Table 6. Measures of genetic variation within samples of *Fluvidona centralia*. The columns give the mean sample size and mean number of alleles per locus, the percentage of loci where more than one allozyme was detected, the mean observed heterozygosity and Nei's (1978) unbiased estimate of expected heterozygosity. Standard deviations are given in brackets.

Population	Mean sample size per Locus	Mean No. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity Direct-count	Mean heterozygosity HdyWbg expected
1. D70 (Cd11)	3.7 (.2)	1.0 (.0)	4.0	.020 (.020)	.017 (.017)
2. D62 (E1 outflow)	11.7 (.2)	1.0 (.0)	.0	.000 (.000)	.000 (.000)
3. D23A&B (E3)	12.9 (.5)	1.0 (.0)	.0	.000 (.000)	.000 (.000)
4. D53 (F9)	9.3 (.4)	1.0 (.0)	4.0	.003 (.003)	.003 (.003)
5. D13 (Ga1)	12.0 (.0)	1.1 (.1)	12.0	.027 (.016)	.048 (.027)
6. D5 outflow (Ga2)	12.0 (.0)	1.2 (.1)	16.0	.053 (.026)	.062 (.030)
7. D15 (Ga6)	4.0 (.0)	1.0 (.0)	4.0	.020 (.020)	.023 (.023)

Table 7. Gene frequency data for *Dalhousia globosa*. The number of scorded individuals follows the locus name. Identifiable hybrids are listed separately in Ca8 and Cd2.

	Population											
Spring	A1	A2	A3	A8	B1	Cala	Cal	Cal	Cal	Cal	Ca8	Ca8
Station	D4A	D9	D2A	D11	D73	D24	D25	D26	D28	D46	D77	D77(hybrid)
Allozyme												
ADH	4	4	5	2	4	6	15	8	8	8		4
1							.033					
2							.033		.063			
3	.875	1.000	1.000	1.000	1.000	1.000	.933	1.000	.938	1.000		1.000
4	.125											
ALKP	6	10	12	23	19	20	79	57	53	44	21	13
2								.018		.023		.038
3	.333	.400	.375		.237	.925	.082	.070	.047	.136	.571	.500
4	.583	.450	.375	1.000	.553	.075	.418	.518	.396	.375	.095	.038
5	.083	.150	.250		.211		.494	.395	.557	.443	.333	.423
6							.006			.023		
AAT1	6	6	11	9	2	6	52	12	8	8		2
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
AAT2	6	6	11	9	2	6	52	12	8	8		2
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
ENO	8	6	6	9	5	8	35	12	8	8		4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
EST1	6	6	11	22	17	20	76	57	53	44	22	11
1			.182	.045								
2	1.000	1.000	.818	.568	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
3				.023								
5				.364								
EST2	6	6	11	27	17	20	76	57	53	44	22	11
2				.019								
3	1.000	1.000	1.000	.981	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST3	6	6	11	28	17	20	76	57	53	44	22	11
1				.018				.018				
2			.091						.142	.273		
3	1.000	1.000	.909	.982	1.000	1.000	.934	.982	.840	.727	1.000	1.000
4									.019			
5							.066					
FH	6	6	9	8	4	6	37	12	8	8	1	
1				.625								
2	1.000	1.000	1.000	.375	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GAL	6	6	6	32	19	6	36	24	20	20	1	
1				.031			.083					
2	1.000	1.000	1.000	.969	1.000		.917	1.000	1.000	1.000	1.000	
3						1.000						
GPD	6	6	10	8	4	6	38	12	8	8	1	
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GPI	6	6	6	28	18	22	82	57	53	44	21	17
1					.056			.009				
2	.500	1.000			.444		.012	.079	.689	.659		
3	.250						.171					
4	.167		1.000	1.000	.500	1.000	.817	.912	.311	.341	1.000	1.000
5	.083											
HK	6	6	6	8	4	6	41	12	8	8		
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
HBDH	8	6	6	28	18	8	44	12	8	8		6
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
IDH1	6	6	10	8	4	20	83	57	53	44	22	11
1											.045	.091
3	1.000	1.000	1.000	1.000	1.000	1.000	.970	1.000	1.000	1.000	.955	.909
4							.030					

	Population											
Spring	A1	A2	A3	A8	B1	Cala	Cal	Cal	Cal	Cal	Ca8	Ca8
Station	D4A	D9	D2A	D11	D73	D24	D25	D26	D28	D46	D77	D77(hybrid)
Allozyme												
IDH2	6	6	10	8	4	20	83	57	53	44	22	11
2	1.000	1.000	1.000	1.000	1.000	1.000	.994	1.000	1.000	1.000	1.000	1.000
3							.006					
LAL	6	6	6	32	19	20	57	57	53	44	6	5
1	.167	.167					.009					
2	.833	.833	1.000	.859	.895	1.000	.772	1.000	1.000	1.000	1.000	1.000
3				.141	.105		.219					
LAP	6	6	15	30	21	20	74	57	53	44	22	11
1			.033					.009				
2	1.000	1.000	.967	.950	.976	1.000	.993	.991	1.000	1.000	1.000	.500
3				.050	.024		.007					.500
LGG1	6	6	10	30	17	20	35	51	47	41	4	3
1	1.000	1.000	1.000	1.000	.971	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2					.029							
LGG2	6	6	12	28	17	16	26	37	32	30	4	3
2		.167	.125	.821	.088	.938	.019	.068	.484	.933	.500	1.000
3			.167		.118		.019		.453	.050		
4							.077				.250	
5	.167	.167	.042	.036	.088							
6	.833	.667	.500	.143	.324	.063	.538	.865	.063	.017	.250	
MDH1			.167		.382		.346	.068				
1	8	6	6	28	18	22	75	57	53	44	21	17
2							.007					
3	.938	1.000	1.000	1.000	.972	1.000	.993	1.000	1.000	1.000	1.000	1.000
MDH2	.063				.028							
1	8	6	6	28	18	22	75	57	53	44	21	17
MPI1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
1	8	6	6	9	3	6	46	12	8	8		6
MPI2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
1	8	6	6	9	3	6	46	12	8	8		6
PPR	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
2	8	6	6	23	3	20	62	57	53	44	12	12
3						.050	.008					.167
4	1.000	1.000	.833	.913	1.000	.925	.952	.991	.981	1.000	1.000	.833
PGD			.167	.087		.025	.040	.009	.019			
2	8	6	6	28	18	22	78	57	53	44	21	17
3					.028							
4	1.000	1.000	1.000	1.000	.972	1.000	.994	1.000	1.000	1.000	1.000	1.000
PGM1							.006					
2	8	6	6	28	18	22	79	57	53	44	21	17
3							.006					
4	1.000	1.000	1.000	1.000	1.000	1.000	.962	.991	1.000	1.000	1.000	1.000
PGM2							.032	.009				
1	8	6	6	28	18	22	79	57	53	44	21	17
2									.009			
3	.938	.417	.500	.089	.778	.955	.361	.368	.934	.977	1.000	1.000
SDH1	.063	.583	.500	.911	.222	.045	.639	.632	.057	.023		
1	6	6	10	21	16	6	25	8	8	8		2
2			.400	.071	.375		.940	1.000	1.000	.813		
SDH2	1.000	1.000	.600	.929	.625	1.000	.060			.188		1.000
1	6	6	10	22	16	6	25	8	8	8		2
2			.050	.250	.313	.917	.040					1.000
TPI	1.000	1.000	.950	.750	.688	.083	.960	1.000	1.000	1.000		
1	8	6	6	9	3	8	48	12	8	8		6
2								.167				
UPDG	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.833	1.000	1.000		1.000
1	4	4	9	3	2	6	9	8	8	8		
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		

	Population											
Spring	Ca9	Cb2	Cb2	Cc1	Cc3	Cd1	Cd1	Cd1	Cd1	Cd2	Cd2(hybrid)	Cd8
Station	D64	D51	D52	D59	D61	D40	D43	D41	D42	D80	D80	D72
Allozyme												
ADH	6	10	5	4	4	7	6	4	4	4	4	4
2			.100		.125					.125	.125	
3	1.000	1.000	.700	1.000	.875	1.000	.917	1.000	1.000	.875	.875	1.000
4			.200				.083					
ALKP	51	14	9	10	7	12	10	10	5	5	4	8
2			.167		.071	.083	.050					
3		.214	.111		.429	.208	.250	.100	.200			
4	.235	.679	.500	.600		.208	.300	.650	.200	.300	.625	.938
5	.765	.107	.222	.400	.500	.500	.400	.250	.600	.700	.375	.063
AAT1	6	14	7	6	9	9	8	10	4	3	6	
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
AAT2	6	14	7	6	9	9	8	10	4	3	6	
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
ENO	9	14	6	6	4	7	8	6	4	4	4	6
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	51	12	5	6	9	7	6	10	4	9	15	4
1		.083	.200				.167					
2	.980	.917	.800	1.000	1.000	1.000	.833	1.000	1.000	1.000	1.000	1.000
3	.020											
EST2	51	12	5	6	9	7	6	10	4	9	15	4
2		.083										.125
3	1.000	.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.875
EST3	51	12	5	6	9	7	6	10	4	9	15	4
1						.214	.500		.500			
2							.083				.067	.125
3	1.000	1.000	1.000	1.000	1.000	.571	.417	1.000	.500	1.000	.933	.875
4						.214						
FH	6	12	5	6	9	9	6	6	4		3	6
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GAL	18	12	5	6	9	9	6	6	4	9	15	6
1											.067	
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.933	1.000
GPD	6	14	6	6	9	9	8	8	4		3	6
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GPI	54	12	6	6	4	7	6	6	4	13	17	4
2		.083				1.000	.583		.500	.038	.059	.625
3				.333				.333				
4	1.000	.917	1.000	.667	1.000		.417	.667	.500	.962	.941	.375
HK	6	14	6	6	9	9	8	6	4	3	6	
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000
HBDH	9	12	6	6	4	7	6	6	4	13	16	4
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH1	51	14	6	6	9	9	8	8	4		3	6
2											.167	
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.833	1.000	
IDH2	51	14	6	6	9	9	8	8	4		3	6
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
LAL	50	14	6	6	9	9	8	6	4	9	15	6
1							.125					
2	1.000	1.000	1.000	1.000	1.000	1.000	.750	1.000	.875	1.000	.967	1.000
3							.125		.125		.033	
LAP	51	20	11	6	9	16	14	12	8	7	13	10
2	.961	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.500	.950
3	.039										.500	.050

Spring Station Allozyme	Population A1 D4A	A2 D9	A3 D2A	A8 D11	B1 D73	Ca1a D24	Ca1 D25	Ca1 D26	Ca1 D28	Ca1 D46	Ca8 D77	Ca8 D77(hybrid)
LGG1	51	18	10	6	5	16	12	8	8	9	15	6
1	.980	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2	.020											
LGG2	21	14	7	6	5	9	10	9	4	7	13	8
1			.143				.100	.056			.077	
2	.071	.429	.286	.250		.222	.050	.167			.115	1.000
3	.405	.107			.100	.778	.200	.167	.625		.231	
4	.024	.036					.500		.125	.571	.500	
5	.476	.321	.429	.583	.700		.150	.611	.250	.286		
6	.024	.107	.143	.167	.200					.143	.077	
MDH1	54	12	6	6	4	7	6	6	4	13	16	4
1		.042	.333									
2	1.000	.958	.667	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH2	54	12	6	6	4	7	6	6	4	13	16	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI1	9	12	6	6	4	7	6	6	4	4	4	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI2	9	12	6	6	4	7	6	6	4	4	4	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PPR	54	12	6	6	4	7	6	6	4	4	4	2
3	1.000	.833	.833	.750	1.000	.857	.750	1.000	.875	1.000	1.000	1.000
4		.167	.167	.250		.143	.250		.125			
PGD	54	12	6	6	4	7	6	6	4	13	16	4
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM1	54	12	6	6	4	7	6	6	4	13	16	4
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM2	54	12	6	6	4	7	6	6	4	13	16	4
2	.565	.917	1.000	1.000	.625	.786	1.000	.667	.875	.885	.875	1.000
3	.435	.083			.375	.214		.333	.125	.115	.125	
SDH1	6	14	8	4	10	16	10	8	8	6	14	10
1		.357	.188	.375	.500	.563	.600	.438	.500	.333	.179	
2	1.000	.643	.813	.625	.500	.438	.400	.563	.500	.667	.821	1.000
SDH2	6	14	8	4	11	16	10	8	8	6	14	10
1	.250	.143		.375	.045			.125		.417	.571	.350
2	.750	.857	1.000	.625	.955	1.000	1.000	.875	1.000	.583	.429	.650
TPI	9	12	6	6	4	7	6	6	4	4	4	4
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
UPDG	3	8	4	4	9	9	4	6	4		2	6
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000

Table 8. Gene frequency data for *Dalhousia harrisi*. The number of individuals follow the locus name.

	Population											
Spring	A1	A2	A3	A6	A8	B1	B2	Ca1	Ca2	Ca3	Ca5	Ca7
Station	D4	D9	D2A	D10	D11	D73	D74	D25	D78	D76	D75	D34
Allozyme												
ADH	4	4	6	6	2	1	4	4	4	8	6	4
2											.333	
3	.875	.875	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.667	1.000
4	.125	.125										
ALKP	30	32	6	29	5	13	14	45	55	48	54	52
2									.018			
3		.016		.138		.154	.179	.056	.591	.021	.389	.019
4	.967	.984	1.000	.845	1.000	.692	.821	.422	.200	.833	.370	.971
5	.033					.154		.489	.191	.135	.231	.010
6								.033		.010		
7				.017							.009	
AAT1	6	6	5	6	3	4	12	9	8	8	9	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT2	6	6	5	6	3	4	12	9	8	8	9	4
1						.125						
2	1.000	1.000	1.000	1.000	1.000	.875	1.000	1.000	1.000	1.000	1.000	1.000
ENO	4	4	6	4	3	3	8	8	6	10	6	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	26	30	5	25	6	12	10	49	51	46	53	50
1	.442	.233	.900	.180			.250					
2	.558	.767	.100	.820	.833	1.000	.750	1.000	1.000	1.000	1.000	1.000
5					.167							
EST2	26	30	5	25	4	12	10	49	51	46	53	50
2					1.000			.010	.039	.043		
3	1.000	.967	1.000	1.000	1.000	1.000	.990	.961	.957	1.000	1.000	
4		.033										
EST3	26	30	5	25	7	12	10	49	51	46	53	50
1	.019	.017		.040								
2				.040	.071			.010		.174		
3	.981	.983	1.000	.900	.929	1.000	1.000	.990	1.000	.826	1.000	1.000
4				.020								
FH	26	30	5	23	4	3	8	9	6	8	31	4
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GAL	26	30	5	25	8	11	8	9	6	8	33	4
1	.019	.033										
2	.981	.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPD	28	32	5	25	4	3	10	9	6	8	33	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	26	30	6	25	7	12	10	48	51	48	52	50
2									.010		.010	
3						.083		.375				
4	1.000	1.000	1.000	1.000	1.000	.917	1.000	.625	.990	1.000	.990	1.000
HK	6	6	5	6	2	3	6	9	6	8	9	4
2	1.000	1.000	1.000	1.000	1.000	.667	1.000	1.000	1.000	1.000	1.000	1.000
3						.333						
HBDH	26	30	6	25	7	12	8	8	6	8	32	4
1						.708	.875					
2	1.000	1.000	1.000	1.000	1.000	.292	.125	1.000	1.000	1.000	1.000	1.000
IDH1	6	6	5	6	4	3	8	49	51	48	29	50
1								.041				
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.949	1.000	.958	1.000	1.000
4								.010		.042		

Spring	A1	A2	A3	A6	A8	B1	B2	Ca1	Ca2	Ca3	Ca5	Ca7
Station	D4	D9	D2A	D10	D11	D73	D74	D25	D78	D76	D75	D34
Allozyme												
IDH2	6	6	5	6	4	3	8	49	51	48	29	50
1									.010			
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.990	.990	1.000	1.000	1.000
3								.010				
LAL	26	30	5	25	8	11	12	9	21	8	33	20
2	1.000	1.000	1.000	1.000	1.000	.909	.917	.944	1.000	1.000	1.000	1.000
3						.091	.083	.056				
LAP	26	30	11	28	6	12	12	53	55	56	53	54
2								.349		.009		
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.632	1.000	.991	.991	1.000
4								.019			.009	
LGG1	24	28	11	27	8	10	8	9	18	12	33	20
1	1.000	1.000	.909	1.000	1.000	.700	1.000	1.000	1.000	1.000	1.000	1.000
2			.091			.300						
LGG2	24	28	11	23	4	10	10	13	20	14	31	20
2								.077		.036		
3	.479	.536		.543	.250	.100	.250	.077	.075	.464	.323	
4	.521	.464	.909	.457	.750	.850	.750	.808	.925	.500	.677	1.000
5			.091									
6						.050		.038				
MDH1	26	30	6	25	7	12	10	44	51	44	52	50
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.990	1.000
MDH2	26	30	6	25	7	12	10	44	51	44	52	50
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI1	6	6	6	6	3	4	10	8	6	8	8	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI2	6	6	6	6	3	4	10	8	6	8	8	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PPR	6	6	6	4	6	4	8	8	35	6	16	36
2			.167	.500			.063	.143	.167	.094		
3	.750	.917	.750	.125	1.000	1.000	.875	.313	.614	.667	.469	1.000
4	.250	.083	.083	.375			.125	.625	.243	.167	.438	
PGD	26	30	6	25	7	12	10	44	51	44	52	50
2						.208	.100					
3	1.000	1.000	1.000	1.000	1.000	.708	.900	1.000	1.000	1.000	1.000	1.000
4						.083						
PGM1	26	30	6	25	7	12	10	48	51	48	52	50
2							.050			.042	.019	
3	.442	.317	.500	.400	1.000	.958	.950	1.000	1.000	.813	.981	1.000
4	.558	.683	.500	.600		.042				.146		
PGM2	26	30	6	25	7	12	10	48	51	48	52	50
1	.788											
2	.212	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.479	1.000	1.000
3										.521		
SDH1	21	25	11	29	5	10	10	11	10	16	37	8
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SDH2	21	25	11	29	3	10	10	11	10	16	37	8
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
TPI	6	6	6	6	3	4	10	8	6	8	8	4
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
UPDG	4	4	5	4	4	2	8	9	6	8	7	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

					Population							
Spring Station	Ca7 D35	Ca8 D38	Ca8 D77	Ca11 D33	Ca12 D36	Cb4 D81	Cb5 D48	Cb5 D49	Cc1 D59	Cc3 D61	Cc4 D57	Cc8 D69
Allozyme												
ADH	4	6		4	4	12	6	6	4	4	6	7
2											.167	
3	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000	.833	1.000
ALKP	54	25	15	48	54	12	32	6	10	10	26	11
1		.020										
2		.040										.045
3		.060	.567	.073	.028		.094			.050	.115	
4	1.000	.580	.133	.896	.509	1.000	.875	1.000	.750	.100	.673	.909
5		.260	.300	.031	.463		.031		.250	.850	.212	.045
6		.040										
AAT1	8	6	2	10	6	6	6	6	8	11	6	9
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT2	8	6	2	10	6	6	6	6	8	11	6	9
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ENO	6	8		10	6	12	6	6	6	4	6	7
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
EST1	52	25	15	50	52	4	26	6	6	11	22	9
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST2	52	25	15	50	52	4	26	6	6	11	22	9
2		.460	.100	.630					.083			
3	1.000	.540	.900	.370	1.000	1.000	1.000	1.000	.917	1.000	1.000	1.000
EST3	52	27	15	50	52	4	26	6	6	11	22	9
2				.040								
3	1.000	1.000	1.000	.960	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
FH	6	6	2	10	6	6	6	6	6	9	6	9
1	.333								.333			
2	.667	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.667	1.000	1.000	1.000
GAL	6	25	1	10	6	6	26	6	6	9	20	8
1							.673	.417			.450	.938
2	1.000	1.000	1.000	1.000	1.000	1.000	.327	.583	1.000	1.000	.550	.063
GPD	6	6	2	10	6	6	6	6	6	9	6	9
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	52	27	13	50	52	12	28	8	6	6	24	7
2					.115							
3					.010	.125	.357	.563		.167		.214
4	1.000	1.000	1.000	1.000	.875	.875	.643	.438	1.000	.833	1.000	.786
HK	6	6	2	10	6	6	6	6	6	9	6	8
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
HBDH	6	27		10	6	12	28	6	6	6	24	7
1						.500						
2	1.000	1.000		1.000	1.000	.500	1.000	1.000	1.000	1.000	1.000	1.000
IDH1	52	6	15	50	52	6	6	6	6	9	6	9
1			.100									
2					.038			.083				
3	1.000	1.000	.900	1.000	.962	1.000	1.000	.917	1.000	1.000	1.000	1.000
IDH2	52	6	15	50	52	6	6	6	6	9	6	9
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LAL	22	27	8	10	22	6	28	6	6	9	24	8
1							.071					
2	.955	1.000	1.000	.950	.955	1.000	.929	.833	.750	1.000	1.000	1.000
3	.045			.050	.045			.167	.250			
LAP	56	27	15	54	56	6	34	6	6	9	30	16
2				.009		.083						
3	1.000	1.000	1.000	.991	1.000	.917	1.000	1.000	1.000	1.000	1.000	1.000
LGG1	22	27	7	12	20	6	34	6	6	5	30	7
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

	Population											
Spring Station Allozyme	Ca7 D35	Ca8 D38	Ca8 D77	Ca11 D33	Ca12 D36	Cb4 D81	Cb5 D48	Cb5 D49	Cc1 D59	Cc3 D61	Cc4 D57	Cc8 D69
LGG2	22	25	7	11	19	6	32	6	6	5	26	9
2			.571		.026							
3		.820		.182		.083	.656	.667				.667
4	.932	.180	.429	.773	.263		.156		.833	1.000	.962	.111
6	.068			.045	.711	.917	.188	.333	.167		.038	.222
MDH1	52	27	13	46	52	12	28	6	6	6	24	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH2	52	27	13	46	52	12	28	6	6	6	24	7
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI1	8	6		10	6	12	6	6	8	6	6	7
1	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI2	8	6		10	6	12	6	6	8	6	6	7
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
PPR	38	6	11	10	38	12	6	6	6	6	6	7
2		.417	.545	.350	.066	.042						
3	1.000	.250	.455	.350	.934	.958	.583	.417	.417	.750		.643
4		.333		.300			.417	.583	.583	.250	1.000	.357
PGD	52	27	13	46	52	12	28	6	6	6	24	7
1								.083				
2						.625				.083		
3	1.000	1.000	1.000	1.000	1.000	.375	1.000	1.000	.917	.917	1.000	1.000
PGM1	52	27	13	50	52	12	28	6	6	6	24	7
2				.060								
3	1.000	1.000	1.000	.940	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM2	52	27	13	50	52	12	28	6	6	6	24	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SDH1	10	27	2	10	8	6	32	6	6	13	28	15
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SDH2	10	27	2	10	8	6	32	6	6	13	28	15
1	1.000	1.000	1.000	1.000	1.000	.833	1.000	1.000	1.000	1.000	1.000	1.000
2						.167						
TPI	8	8		10	6	10	6	6	8	6	6	7
2	1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
UPDG	4	6	2	8	4	6	4	4	4	9	4	9
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

	Population											
Spring Station Allozyme	Cd1 D40	Cd2 D80	Cd3 D79	Cd5 D63	Cd9 D71	Da1 D56	Da2 D45	Da3 D44	Db1 D31	Db2 D20	Db4 D29A	E1 D6
ADH	5	2	3	6	4	2	4	7	4	4	4	6
2										.750		
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.250	1.000	1.000
ALKP	7	17	8	5	10	8	28	12	8	10	6	24
3	.357				.300	.063		.083		.300		
4	.429	.559	.875	1.000	.700	.938	1.000	.917	1.000	.700	1.000	.688
5	.214	.412	.125									.313
6		.029										
AAT1	6	3	6	5	8	6	6	12	6	10	6	10
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT2	6	3	6	5	8	6	6	12	6	10	6	10
1			.167									
2	1.000	1.000	.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ENO	9	2	5	6	6	6	4	11	6	8	6	8
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	9	32	6	5	6	6	26	12	6	10	6	28
1	.111											
2	.889	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST2	9	32	6	5	6	6	26	12	6	10	6	28
1					.167							
2	.111				.833				.300			
3	.889	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.700	1.000	1.000	
EST3	9	32	6	5	6	6	26	12	6	10	6	28
1												.036
2	.111			.300						.100		
3	.889	.969	1.000	.700	1.000	1.000	1.000	1.000	1.000	.900	1.000	.964
6		.031										
FH	4	3	6	5	6	6	6	12	6	10	6	26
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GAL	6	32	5	5	6	6	30	12	6	10	6	28
1		.031		.900		.667	.517			.800		.107
2	1.000	.969	1.000	.100	1.000	.333	.483	1.000	1.000	.200	1.000	.893
GPD	6	3	6	5	6	6	6	12	6	10	6	28
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	7	30	5	8	6	6	26	11	6	10	6	26
2	.143	.133		.063				.136				
3			.300	.125		.833	.538		.167	.300	.083	
4	.857	.867	.700	.813	1.000	.167	.462	.864	.833	.700	.917	1.000
HK	6	3	5	5	6	6	6	12	6	6	6	6
2	1.000	1.000	1.000	1.000	1.000	.833	1.000	1.000	.667	1.000	1.000	1.000
3						.167			.333			
HBDH	7	31	5	6	6	6	26	11	6	10	6	28
1												.196
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.804
IDH1	6	3	6	5	6	6	6	12	6	10	6	8
2		.167										.125
3	1.000	.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.875
IDH2	6	3	6	5	6	6	6	12	6	10	6	8
1												.125
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.875
LAL	6	32	5	5	6	6	26	12	6	10	6	28
1	.167											
2	.833	.969	.700	.800	1.000	.917	1.000	.667	.833	.700	.667	1.000
3		.031	.300	.200		.083		.333	.167	.300	.333	

	Population											
Spring Station Allozyme	Cd1 D40	Cd2 D80	Cd3 D79	Cd5 D63	Cd9 D71	Da1 D56	Da2 D45	Da3 D44	Db1 D31	Db2 D20	Db4 D29A	E1 D6
LAP	11	32	9	5	10	6	30	19	6	14	10	28
2				.100				.053				
3	1.000	1.000	1.000	.900	1.000	1.000	1.000	.947	1.000	1.000	1.000	1.000
LGG1	9	32	6	5	6	6	30	15	6	10	8	24
1	.889	1.000	.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.792
2	.111		.167									.208
LGG2	4	32	6	5	8	6	32	11	6	8	3	24
2		.125									.500	
3	.125	.094	.250	.700	.688	.417	.297	.136	.083			.417
4	.500	.750	.583		.313		.125	.636	.250	.688	.167	.563
5	.125	.016										
6	.250	.016	.167	.300		.583	.578	.227	.667	.313	.333	.021
MDH1	7	31	5	6	4	6	26	11	6	10	6	26
1	.143											
2	.857	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH2	7	31	5	6	4	6	26	11	6	10	6	26
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI1	7	2	5	6	6	6	6	11	6	10	6	10
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI2	7	2	5	6	6	6	6	11	6	10	6	10
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PPR	7	2	5	6	4	6	6	11	6	8	6	10
2			.300				.250		.583	.688	.667	
3	.500	1.000	.400	.667	.875	.417	.333	.909	.083		.333	.600
4	.500		.300	.333	.125	.583	.417	.091	.333	.313		.400
PGD	7	31	5	6	6	6	26	11	6	10	6	26
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM1	7	31	5	6	6	6	26	11	6	10	6	30
1												.067
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.933
PGM2	7	31	5	6	6	6	26	11	6	10	6	30
1									.250	.700		.033
2	1.000	.919	1.000	1.000	1.000	1.000	1.000	1.000	.750	.300	1.000	.967
3		.081										
SDH1	9	28	6	5	10	6	30	15	6	10	4	26
1		.232										
2	1.000	.768	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SDH2	9	28	6	5	10	6	30	15	6	10	8	26
1	1.000	.625	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.938	1.000
2		.375									.063	
TPI	7	2	5	6	6	6	6	11	6	10	6	10
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
UPDG	2	2	4	3	6	4	4	8	4	6	4	6
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

	Population											
Spring	E2	E5	E7	E8	F1	F2	Ga2	Ga3	Ga4	Ga6	H1	H3
Station	D7	D8	D17A	D18	D54	D55	D5A	D14	D12	D16	D1	D19
Allozyme												
ADH	4	8	4	6	4	4	6	16	6	8	4	6
2						.125						.250
3	1.000	1.000	1.000	1.000	1.000	.750	1.000	1.000	1.000	1.000		.333
4						.125					1.000	.417
ALKP	10	38	22	34	32	29	29	36	26	19	30	25
3		.013	.023		.031	.034	.034			.132		
4	.850	.987	.977	1.000	.969	.948	.914	.986	1.000	.816	1.000	1.000
5	.150					.017	.052	.014		.053		
AAT1	10	14	10	10	8	8	10	20	6	21	8	7
1	1.000	1.000	1.000	1.000	1.000	1.000	.950	1.000	1.000	.952	1.000	1.000
2							.050			.048		
AAT2	10	14	10	10	8	8	10	20	6	21	8	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ENO	8	12	8	6	8	6	10	20	6	18	8	10
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	10	28	24	30	28	25	34	38	26	21	28	23
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST2	10	26	22	28	28	25	34	38	26	21	26	23
1									.013			
2		.962	.068	.179	.714		.941	.842	.481	.333	.500	.370
3	1.000	.038	.932	.821	.286	1.000	.059	.145	.519	.667	.500	.630
EST3	10	28	24	30	28	25	34	38	26	21	28	23
1			.042									.022
2		.036			.018				.019			
3	.900	.964	.958	1.000	.982	1.000	1.000	1.000	.981	.976	1.000	.978
4										.024		
7	.100											
FH	8	26	20	28	28	8	34	40	26	21	27	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GAL	8	26	26	26	28	29	36	42	28	21	25	27
1	.063		.712	.038	.875	.724					.120	.778
2	.938	1.000	.288	.962	.125	.276	1.000	1.000	1.000	1.000	.880	.222
GPD	10	30	24	30	28	8	36	42	28	21	27	7
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	10	30	24	30	28	25	36	42	28	21	26	28
3	.450	.017	.021			.060						.268
4	.550	.983	.979	1.000	1.000	.940	1.000	1.000	1.000	1.000	1.000	.732
HK	6	10	6	6	6	6	10	20	6	18	6	5
1										.028		
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.972	1.000	1.000
HBDH	10	28	24	28	28	25	36	42	28	21	28	28
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH1	8	12	8	8	8	8	10	20	6	21	7	7
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH2	8	12	8	8	8	8	10	20	6	21	7	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LAL	8	28	22	28	28	25	36	42	28	21	27	25
1											.037	
2	.875	1.000	1.000	1.000	1.000	1.000	.917	1.000	1.000	.762	.963	1.000
3	.125						.083			.238		
LAP	8	36	22	32	28	25	36	42	28	23	27	25
2	.063							.024		.043		
3	.938	1.000	1.000	1.000	1.000	.980	.972	.976	1.000	.957	1.000	1.000
4						.020	.028					

	Population											
Spring	E2	E5	E7	E8	F1	F2	Ga2	Ga3	Ga4	Ga6	H1	H3
Station	D7	D8	D17A	D18	D54	D55	D5A	D14	D12	D16	D1	D19
Allozyme												
LGG1	8	34	20	32	28	25	34	42	26	20	27	23
1	1.000	.882	1.000	1.000	.982	1.000	.368	.726	1.000	.950	1.000	1.000
2		.118			.018		.632	.274		.050		
LGG2	8	26	22	26	24	25	35	42	26	18	22	23
3	.063	.077	.023	.038			.071	.060	.385	.194	.545	
4	.188	.846	.705	.288	.500	.200	.929	.940	.500	.778	.432	
5	.063											
6	.688	.077	.273	.673	.500	.800			.115	.028	.023	1.000
MDH1	10	30	24	30	28	25	36	42	28	21	28	28
1								.012				
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.964	1.000	1.000	1.000	1.000
3								.024				
MDH2	10	30	24	30	28	25	36	42	28	21	28	28
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI1	10	14	10	10	8	8	10	20	6	21	8	8
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI2	10	14	10	10	8	8	10	20	6	21	8	8
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PPR	10	14	10	8	30	8	10	20	6	18	8	9
1				.063								
2	.200	1.000	.100	.250	.183	.250	.700	.500	.333	.361		
3	.650		.550	.250	.750	.438		.250		.528	.500	.556
4	.150		.350	.438	.067	.313	.300	.250	.667	.111	.500	.444
PGD	10	26	24	28	26	25	36	42	28	21	26	28
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.976	1.000	1.000
4										.024		
PGM1	10	30	24	28	28	25	36	42	28	21	26	28
1	.100	.050		.232					.179		.019	.018
2	.050			.464			.319	.786	.357	.048	.192	
3	.850	.950	1.000	.304	1.000	1.000	.681	.214	.464	.952	.788	.982
PGM2	10	30	24	30	28	25	36	42	28	21	28	28
1	.150	.767	.354		.054		.014					
2	.850	.233	.646	1.000	.946	1.000	.986	1.000	1.000	1.000	1.000	1.000
SDH1	6	34	22	30	30	23	34	40	28	19	28	23
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SDH2	6	34	20	30	30	23	34	40	28	19	28	23
1	.750	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2	.250											
TPI	10	14	10	10	8	8	10	20	6	21	8	10
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
UPDG	6	10	6	6	6	6	10	16	6	16	5	7
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 9. Gene frequency data for *Fluvidona centralia*. The number of individuals follow the locus name.

	Population						
Spring	Cd11	E1	E3	F9	Ga1	Ga2	Ga6
Station	D70	D62	D23(A+B)	D53	D13	D5B	D15
Allozyme							
AAT1	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT2	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ALKP	4	12	10	8	12	12	4
1						.167	
2	1.000	1.000	1.000	1.000	.417	.708	1.000
3					.583	.125	
ENO	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	3	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST2	1	8	8	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	.875	1.000
2						.125	
EST3	1	8	8	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	4	12	12	8	12	12	4
1							
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPT1	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPT2	4	12	16	12	12	12	4
1	1.000	1.000		1.000			
2			1.000		1.000	1.000	1.000
GPD	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
HBDH	4	12	12	8	12	12	4
1	.750						
2	.250	1.000	1.000	1.000	1.000	1.000	1.000
IDH1	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH2	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH1	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH2	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PPR	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM1	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2							
PGM2	4	12	12	8	12	12	4
1							
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000
3							
6PGD	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	.250	.417	1.000
2					.750	.583	

	Population						
Spring Station Allozyme	Cd11 D70	E1 D62	E3 D23(A+B)	F9 D53	Ga1 D13	Ga2 D5B	Ga6 D15
SDH1	4	12	16	12	12	12	4
1							
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000
SDH2	4	12	16	12	12	12	4
1							
2	1.000		1.000	.958	.167	.208	.500
3		1.000		.042	.833	.792	.500
TPI	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
UDPG	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000

NOTICE
R. Viader Collection

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Generally, the whereabouts of the Mauritian collections described by R. Viader (1938, 1951) are unknown to the scientific community. Part of the collections on which Viader (1951) was based was recently found in private hands in Mauritius. Mr. Owen Griffiths of Senneville, Mauritius, while visiting Mr. F.V. Descroizilles in search of terrestrial molluscs, was shown a collection of smaller marine molluscs purchased from the late R. Viader's son in about 1982. The collection was in poor shape, stored in a garage and ravaged by insects, but some material had slips with plate and figure numbers. Mr. Griffiths obtained the material and presented it to the Australian Museum in 1993. He was told that larger shells had been sold to local collectors, that acquired by Mr. Descroizilles being subsequently resold. Other material is held privately by Viader descendants now in the United Kingdom (pers. comm. D.G. Herbert, Natal Museum).

While the material now in the Australian Museum had no locality labels, many had individual identification labels and some had citation labels. Some labels were now separated from relevant specimens. The few lots which were clearly recognisable as not belonging to the Mauritian fauna were accompanied by non-Mauritian locality labels. More than 800 lots of small marine molluscs have now been distinguished. Types for 19 of the 27 new species level taxa in the 1951 paper, 8 other figured lots and 11 cited lots have been identified. No specimens identifiable with material included in Viader (1938) could be identified. Also, a lot from Oubatche, New Caledonia already held in the Australian Museum (C.4037) and cited by Hedley (1899) is recognised as a syntypic lot of *Contumax hedleyi* Viader, 1951, a previously unrecognised (eg. Houbrick, 1992) synonym of *Cerithium nodulosum* Bruguière, 1792.

Types distinguished (all Viader, 1951):

Arcidae: *Arca acupicta,* holotype, C.305529, 1 valve. *Arca approximata,* holotype, C.305531, 1 valve. *Arca elegans,* syntypes, C.305532, 2 valves. *Arca lienardi,* syntypes, C.305533, 3 valves. *Petunculus ornatus,* holotype, C.305534, 1 valve.

Mytilidae: *Brachydontes (Hormomya) ramulosus,* syntypes, C.305542, 8 valves.

Lucinidae: *Lucina (Phacoides) virginiae,* holotype, C.305546, 1 pair valves. *Lucina (Bellucina) louisensis,* syntypes, C.305545, 3 valves.

Carditidae: *Cardita vinsoni,* syntypes, C.305543, many valves. *Cardita transclathratum,* syntypes, C.305554, 16 valves. *Cardita vaughani,* syntypes, C.305544, many valves.

Veneridae: *Dosinia miticula,* syntypes, C.305553, many valves. *Chione (Timoclea) concinna,* syntypes, C.305552, 4 valves. *Chione similicentrifuga,* syntypes, C.305624, 4 valves.

Tellinidae: *Tellina patagiata mauritiana,* syntypes, C.305551, 6 valves.

Psammobiidae: *Psammobia flabellum,* syntypes, C.305557, 5 valves.

Turbinidae: *Leptothyra morini,* 3 syntypes, C.305556.

Columbellidae: *Pyrene parvula,* holotype, C.305615. *Pyrene perparvula,* 11 possible syntypes, C.305617.

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Moll. Res. 17: 111–114 (1996).

A note on the egg capsule of *Nodilittorina unifasciata* from eastern Australia.

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Keywords: Littorinidae, *Nodilittorina*, egg capsule, Australia, New Zealand

Introduction

This is the first published description of the planktonic egg capsule of *Nodilittorina unifasciata* (Gray, 1826), a common littorinid snail living high on rocky shores of southern Australia from northern New South Wales to southwestern Western Australia. It is a dominant animal on many shores and has been the subject of many biological and ecological studies (– as *Littorina unifasciata*: Branch & Branch, 1981; Chen & Richardson, 1987; Underwood, 1974; Underwood & Chapman, 1989; Wells, 1984). The transfer of this species to *Nodilittorina* was proposed by Bandel & Kadolsky (1982), and supported by Reid (1989). Our understanding of the life history of *N. unifasciata,* is based on histological studies of the gonad (Underwood, 1974) and structure of the pallial oviduct (Reid, 1989). Murray (in an unpublished letter in Pilkington, 1971) reports that both *N. unifasciata* and *N. praetermissa* (May, 1908) liberate egg capsules (presumably planktonic) with the veliger stage already well-developed, and these were also studied by Tin Nwe (1974). The planktonic egg capsules of *N. antipoda* (Philippi, 1847) (as *Melarapha oliveri* Finlay, 1930), a supposed subspecies of *N. unifasciata* from New Zealand, and another New Zealand species, *N. cincta* (Quoy & Gaimard, 1833), have been described (Pilkington, 1971).

Many studies have shown that the ability to identify accurately littorinid egg capsules from inshore plankton samples, or high tidal pools, is a valuable tool in studying the life history and ecology of these animals (Habe, 1956; Kojima, 1957a,b, 1958; Borkowski, 1971; Pilkington, 1971; Ohgaki, 1981). Reid (1989) has discussed the value of capsule morphology in understanding the phylogeny and taxonomy of the Littorinidae.

Methods & Results

Snails ranging in shell height from 15–19mm were collected from supra–littoral aggregations at Harbord, Sydney, NSW (at low tide, 6 October 1995) and placed in groups of 12–15 in glass jars half filled with sea water, at 4pm the same day. The jars were left until 9am, 9 October, when four out of six jars contained a few free swimming veligers and up to 10–12 egg capsules (Figs 1, 2c). The seawater was changed daily and a similar number of eggs were laid each day, until observations ceased 10 days later. In a few cases 3–4 capsules adhered together in a string for a few hours after hatching but separated with moderate water movement. No attempt was made to time or study development, but eggs were laid at the single cell stage and within 12 hours were fully developed veligers, hatching within 18 hours. The ambient room temperature was maintained between 22–24°C. The observation by Murray (in Pilkington, 1971) that capsules were laid with fully developed veligers was not confirmed.

Egg capsules appear disc, or dome-shaped ('cupola' type of Reid, 1989), and almost completely transparent. There is a prominent central dome on the convex face of the capsule, and there is a central swelling on the concave face to accommodate the egg. During hatching, the veliger breaks free in this

Figure 1. Pelagic egg capsules of *Nodilittorina unifasciata* laid by snails collected at Harbord, Sydney, October 1995. Capsule diameter 240 µm. Photo: G.Avern.

region of the concave face. The convex face of the capsule is perhaps best described as a dome, with a somewhat roughened surface, surrounded by a wide cylindrical skirt. There is a distinct median ridge around the broad outer edge of the skirt.

Because of the extreme transparency of the capsule, external sculpture is only visible by manipulating the direction of incident light falling on the capsule. There is clearly a median ridge on the outer half ('skirt') of the capsule. In some angles of light, under the microscope, it is possible to consider that there is a 'thickening', or rounded ridge, at both the outer and inner edges of the capsule skirt. The widest diameter of the capsule is 240 µm, and the egg diameter approximately 100 µm.

Discussion

Rosewater (1970) suggested that the Australian *N. unifasciata* and a common, similarly coloured New Zealand species, *N. antipoda* (Philippi) (= *Melaraphe oliveri* Finlay), were subspecies. The latter species is found throughout New Zealand, has a characteristic blue and white shell, and is seldom greater than 1cm in height. A comparison of the reported morphology of the planktonic egg-capsules of *N. antipoda*, and a second New Zealand species, *Nodilittorina cincta* (Pilkington, 1971), with the egg-capsules of *N. unifasciata* from Australia, suggests that either the two 'subspecies' are distinct species or that Pilkington (1971) misidentified the capsules she described.

The egg capsule of *N. cincta*, as described by Pilkington (1971)(Fig. 2A), is quite similar to that of *N. unifasciata*, while the egg capsule of *N. antipoda* (as *M. oliveri*) (the supposed subspecies of *N. unifasciata*), is quite different (Fig. 2B). In *N. cincta*, the egg capsule has a broad outer skirt with a distinct ridge, surrounding a central dome-shaped region, similar to *N. unifasciata*. Both are very similar in diameter. In comparison, the egg capsule of *N. antipoda* is much more regularly dome-shaped. Veliger larvae hatch from the capsules of both *N. cincta* and *N. antipoda* 3–4 days after laying (Pilkington, 1971), while I have observed hatching in *N. unifasciata* within 18 hours.

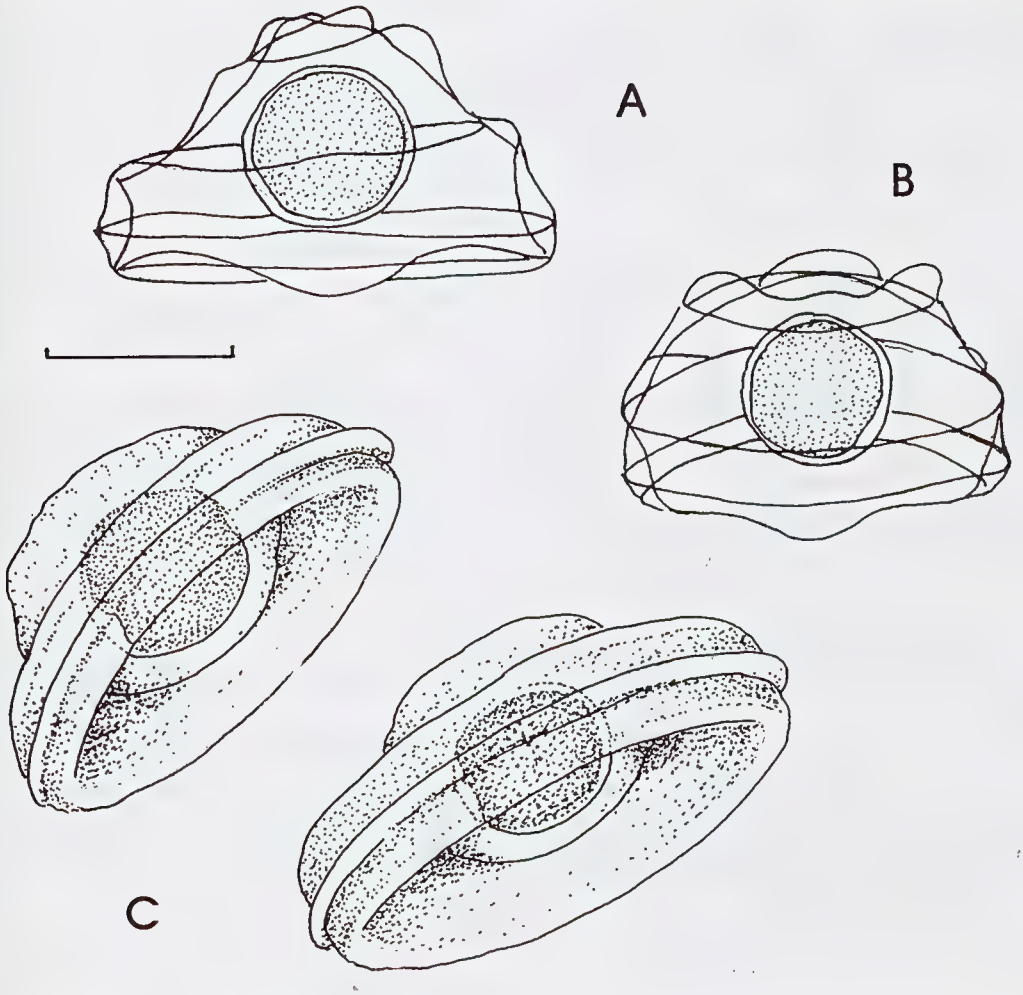

Figure 2. Pelagic egg capsules of *Nodilittorina*. A, *N. cincta*., B, *N. antipoda*., C, *N. unifasciata*. (A,B, after Pilkington, 1971). Scale = 100 µm.

The similarity between the capsules of *N. unifasciata* and *N. cincta*, and their difference in shape to the capsule of *N. antipoda* is puzzling. One would expect that the egg capsules of the two supposed subspecies of *N. unifasciata* would be similar in shape, and different from a second species. Certainly the studies of Japanese species (cited above), and of Caribbean species (Borkowski, 1971) would suggest that egg capsule morphology is species specific (but see Reid, 1986 for contrary view). On the basis of these observations it would seem necessary to restudy the egg capsules of the New Zealand species. The close similarity in egg capsule morphology between the Australian *N. unifasciata* and the New Zealand *N. cincta* suggests that either a misidentification has occurred, or if Pilkington's observations are confirmed, that the two 'subspecies' of *N. unifasciata* are distinct species. This would support Reid's listing (1989) of both *N. unifasciata* and *N. antipoda* as full species (without discussion but on anatomical grounds – D.Reid; *pers.com*).

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Shepherd, S. A. and Cannon, J. 1988. Studies on southern Australian abalone (genus *Haliotis*). X. Food and feeding of juveniles. Journal of the Malacological Society of Australia 9: 21-26.

Kohn, A. J. and Amalsi, K. N. 1993. Comparative ecology of a biogeographically heterogeneous *Conus* assemblage. Pp. 523-538. In: Wells, F. E., Walker, D. I., Kirkman, H. and Lethbridge, R. The Marine Flora and Fauna of Rottnest Island, Western Australia. Western Australian Museum, Perth.

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